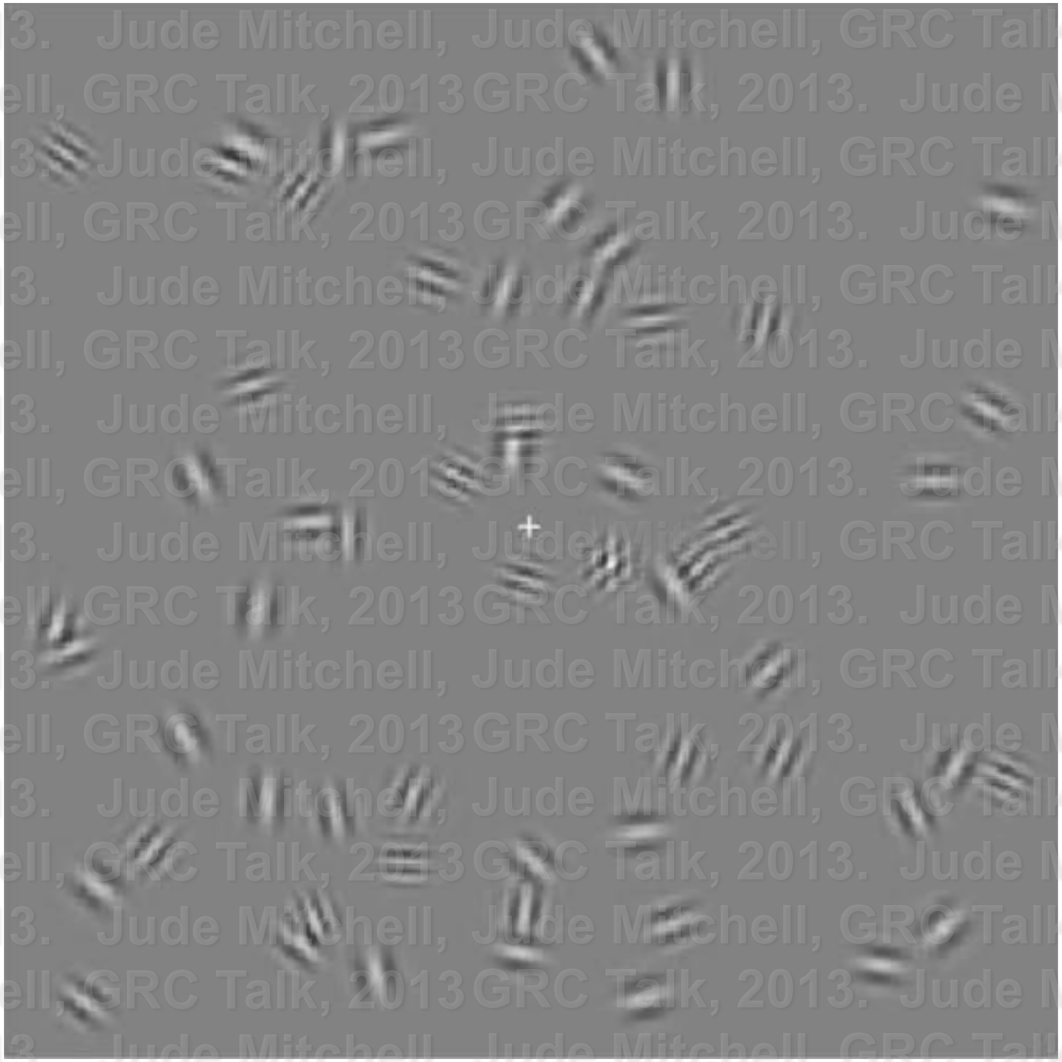
# Teasing apart cortical circuits and the role of attention feedback in sensory processing

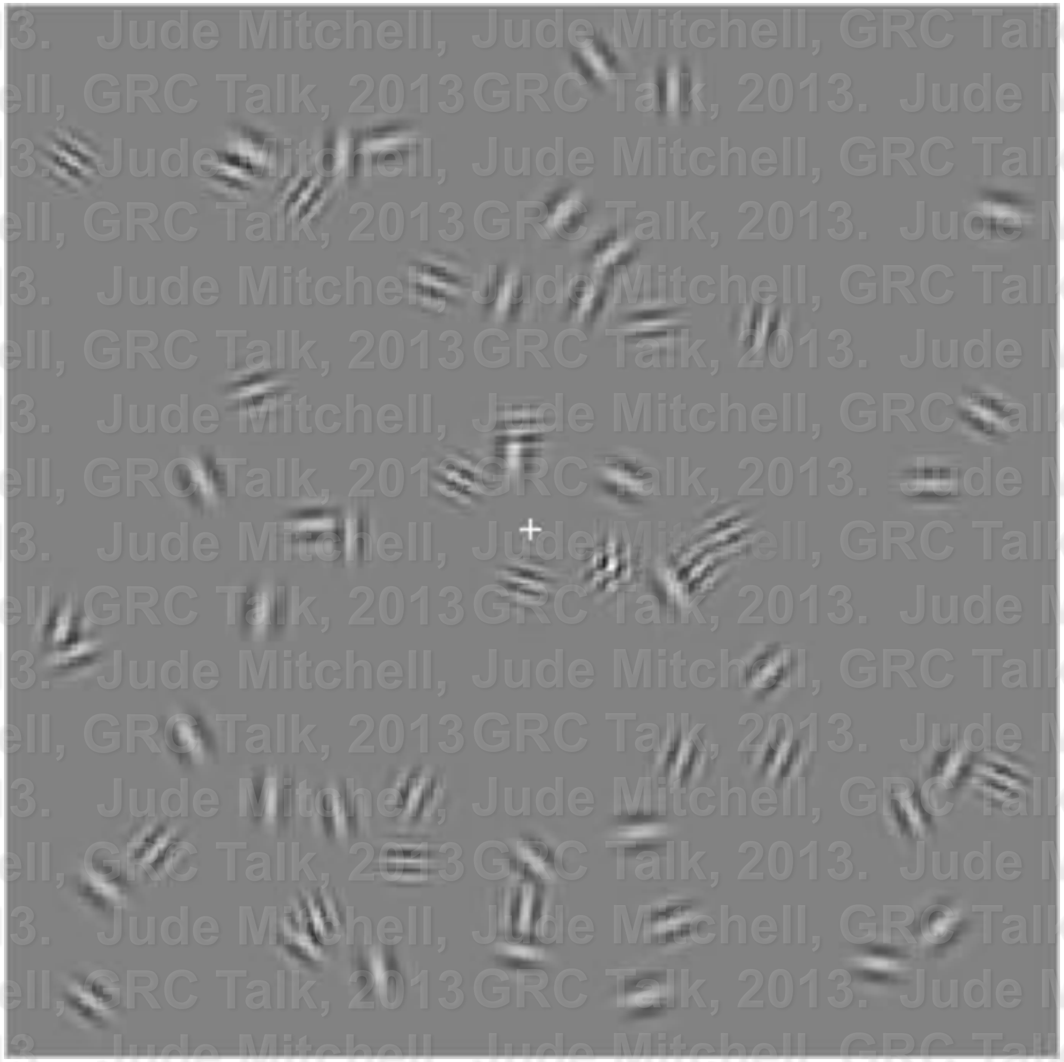

Jude Mitchell

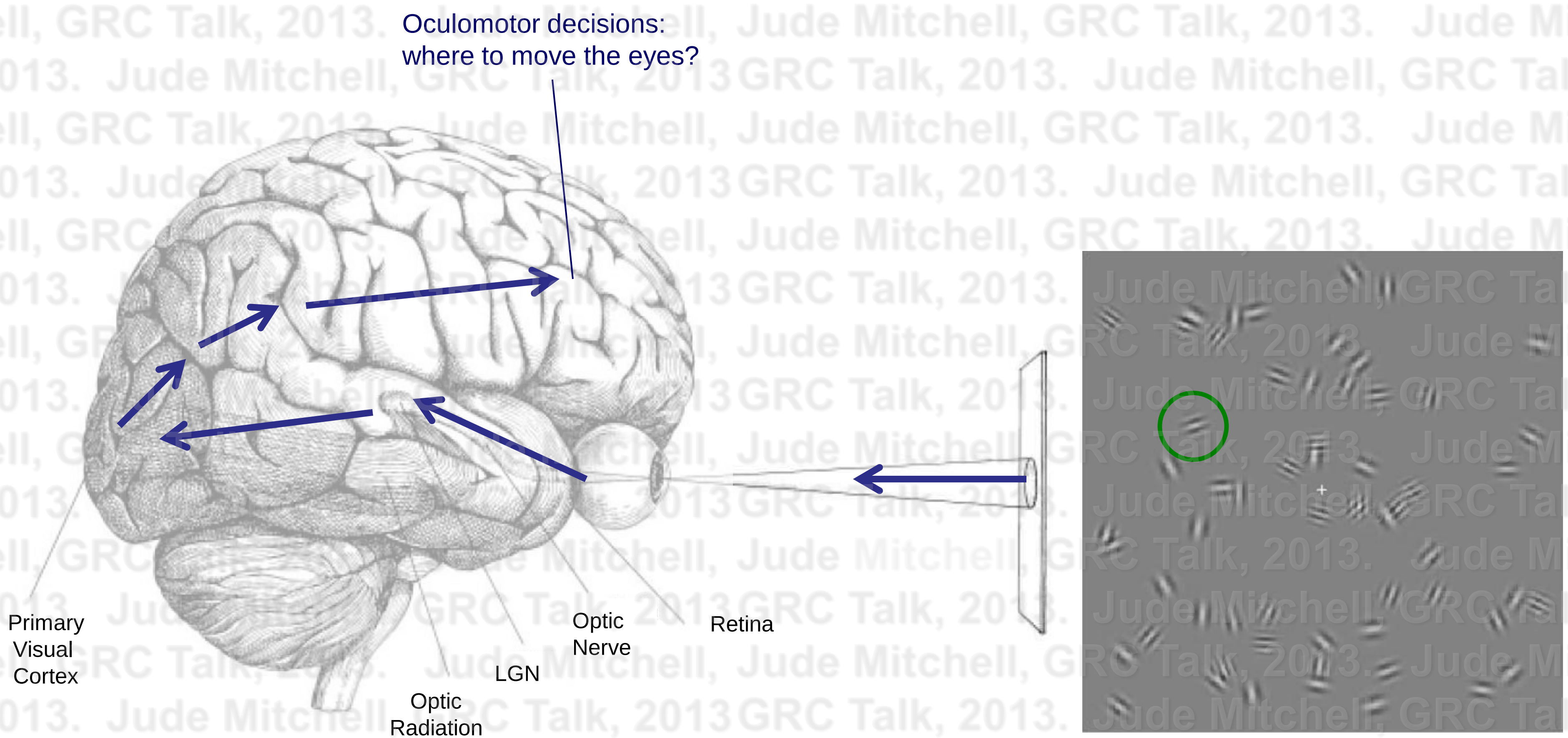
Systems Neurobiology
The Salk Institute
La Jolla, CA

# Change Blindness

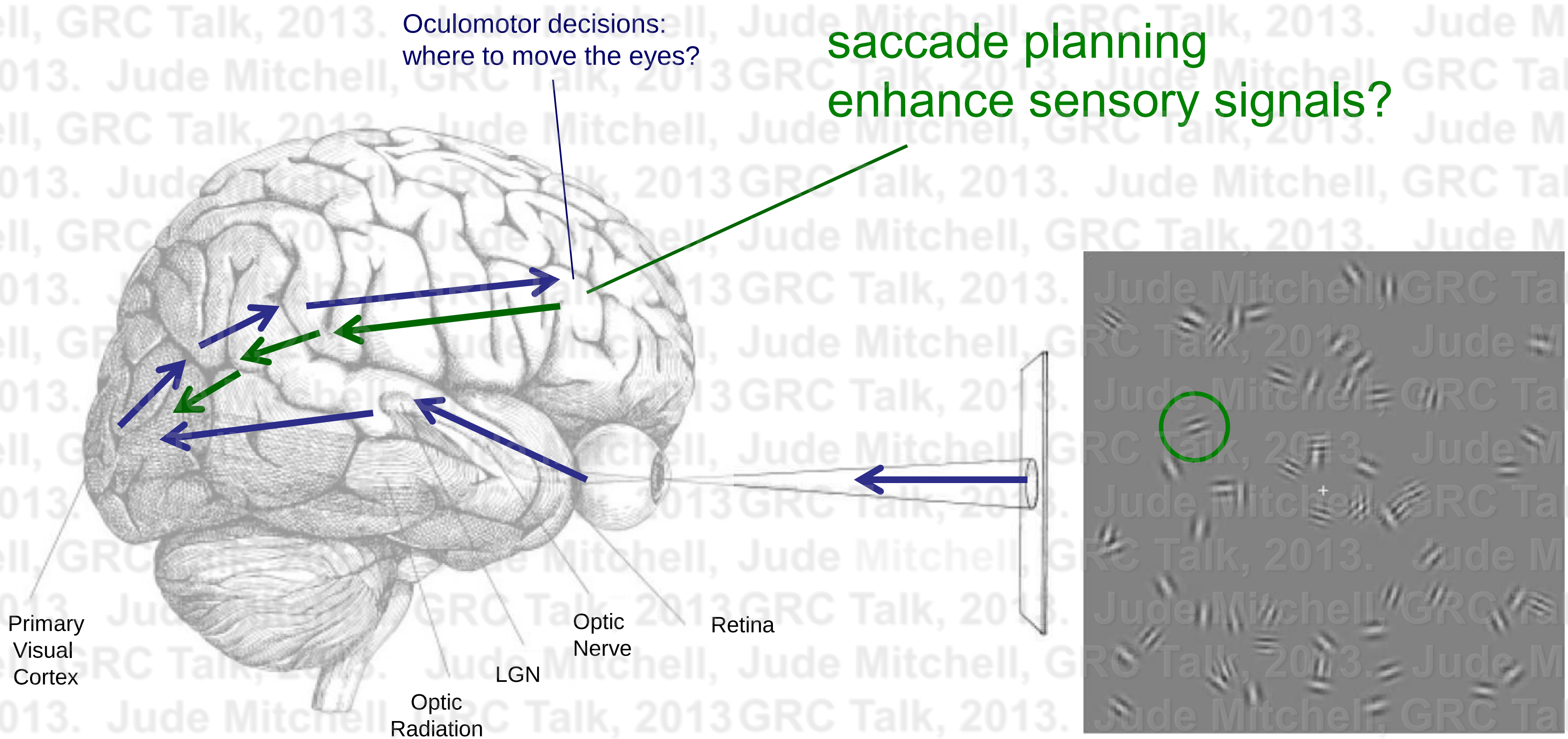


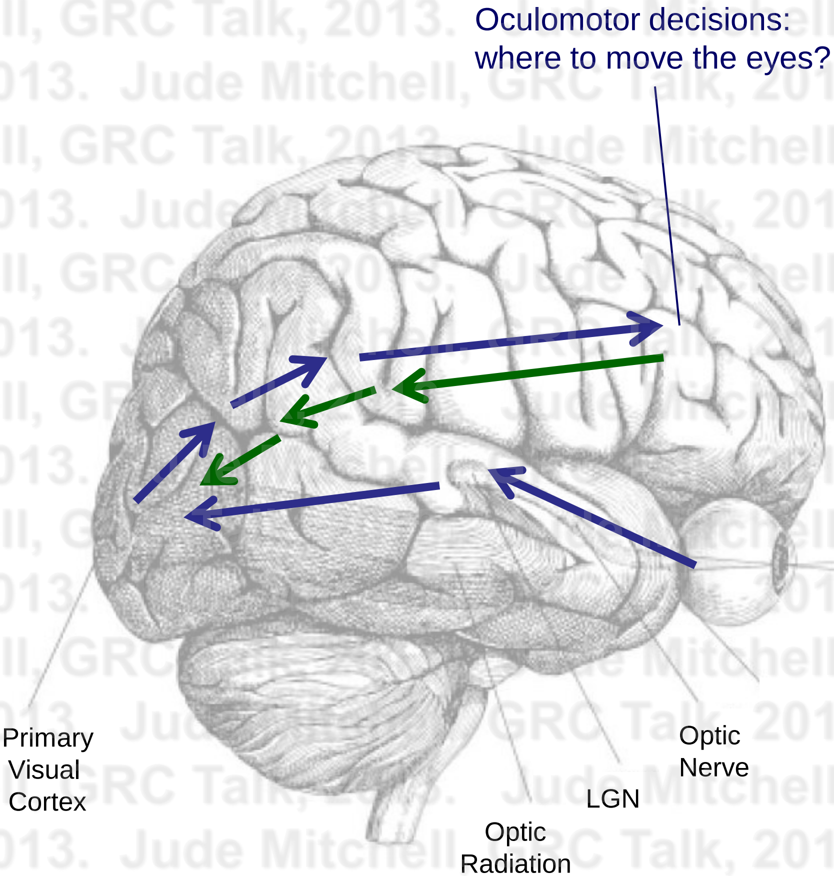
# Change Blindness




Oculomotor decisions:
where to move the eyes?
Primary
Visual
Cortex
Optic
Radiation
LGN
Optic
Nerve
Retina

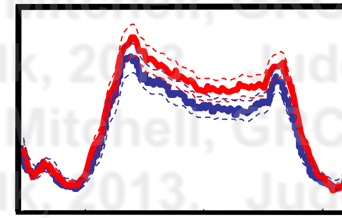
# How does attention or saccade planning enhance sensory signals?



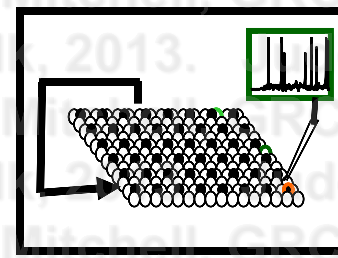



TALK OUTLINE

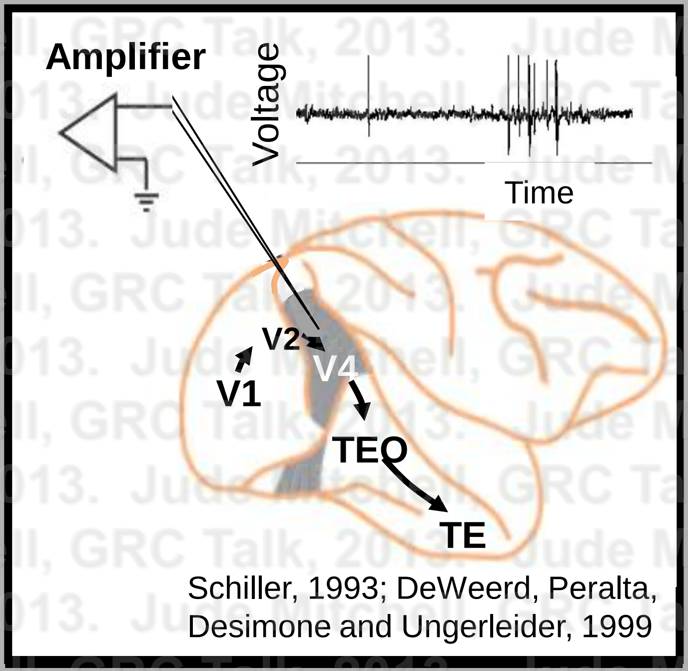
1) Attention modulation of sensory signals in macaque V4



2) A spiking network model of V4 and its predictions

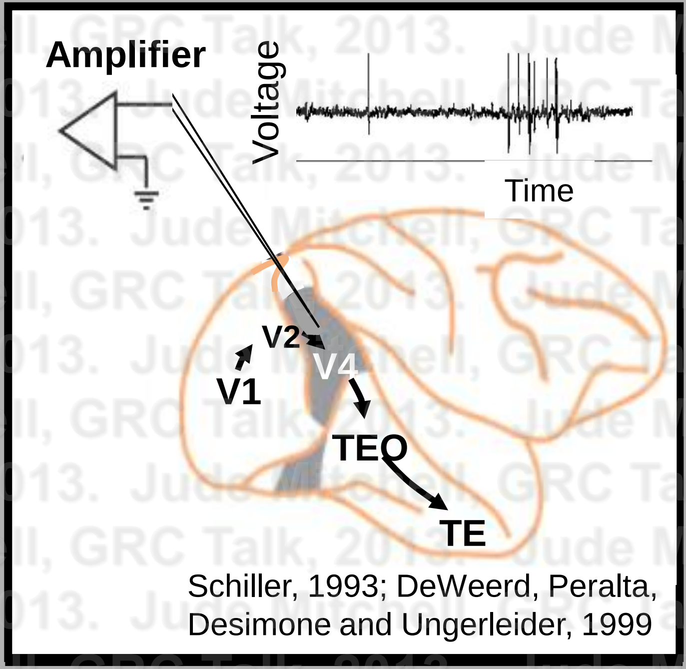


3) Marmosets as a model for visual neuroscience?

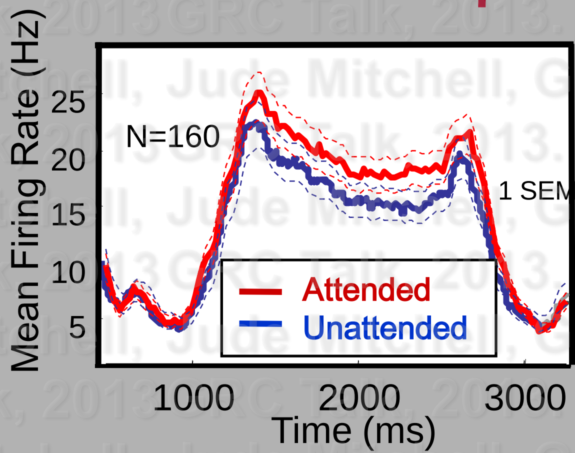



Recordings from macaque V4

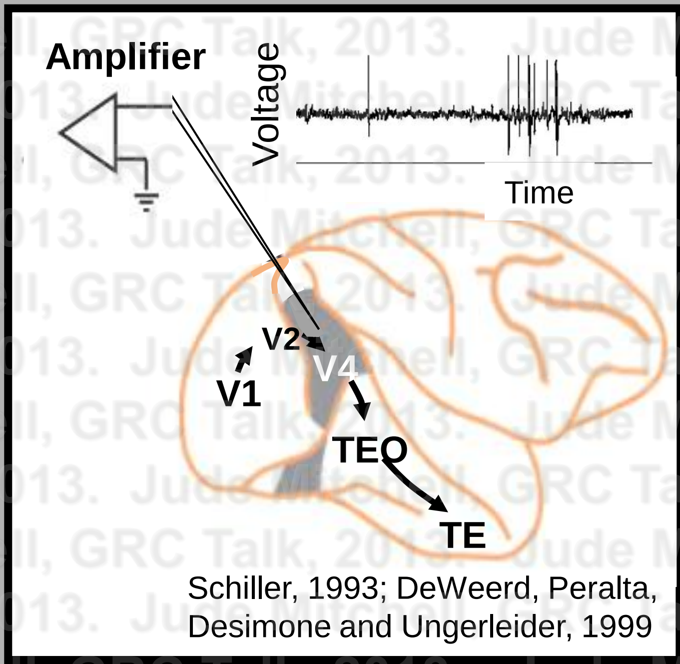
# Attention increases the gain of the visual response



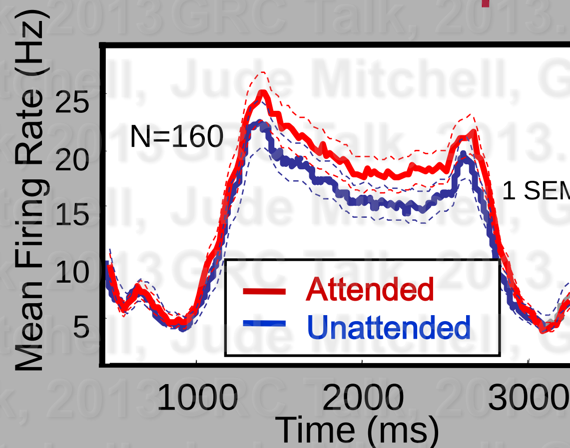

Recordings from macaque V4

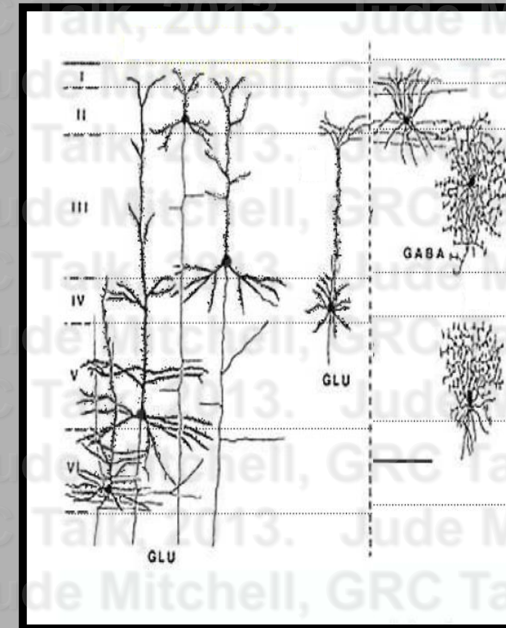


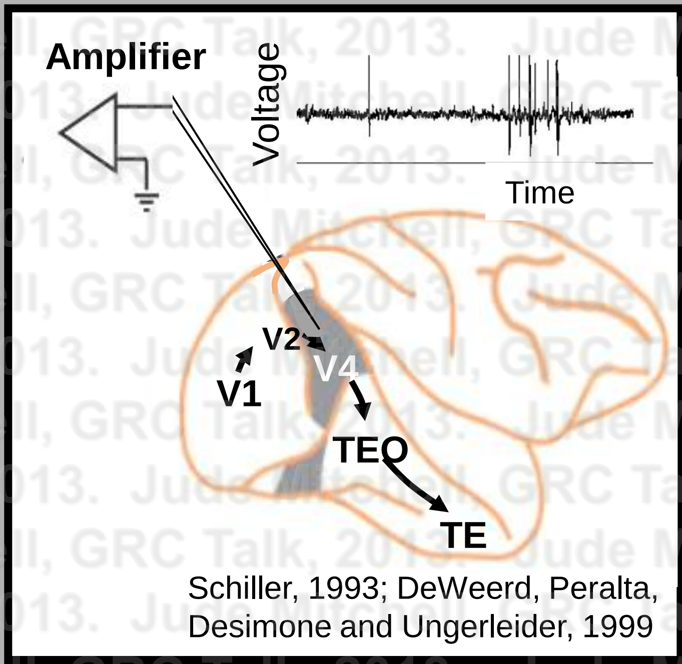
# Attention increases the gain of the visual response



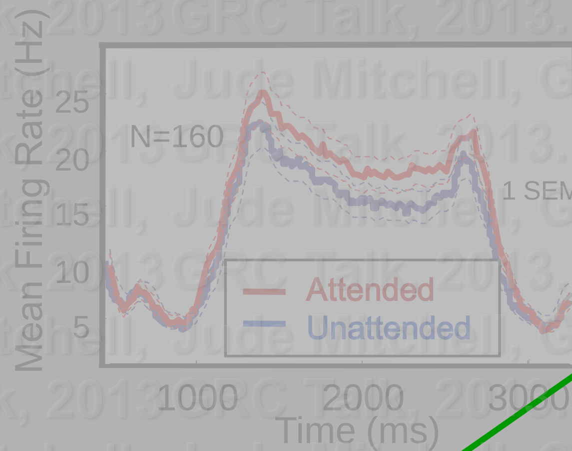

Recordings from macaque V4

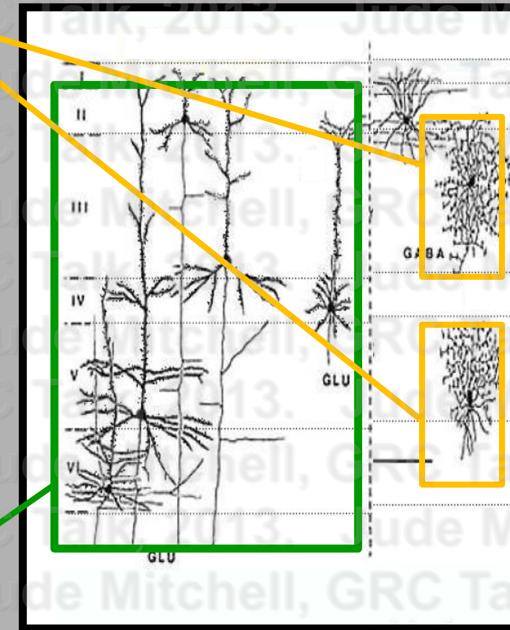


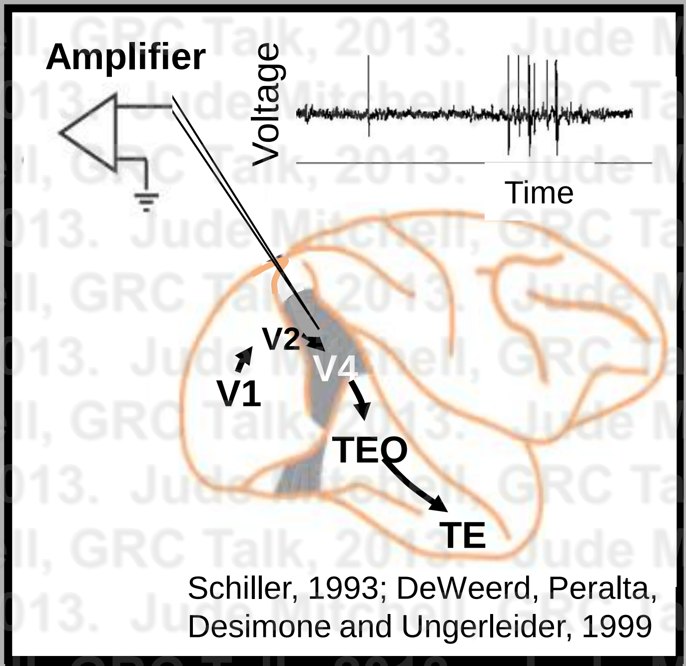





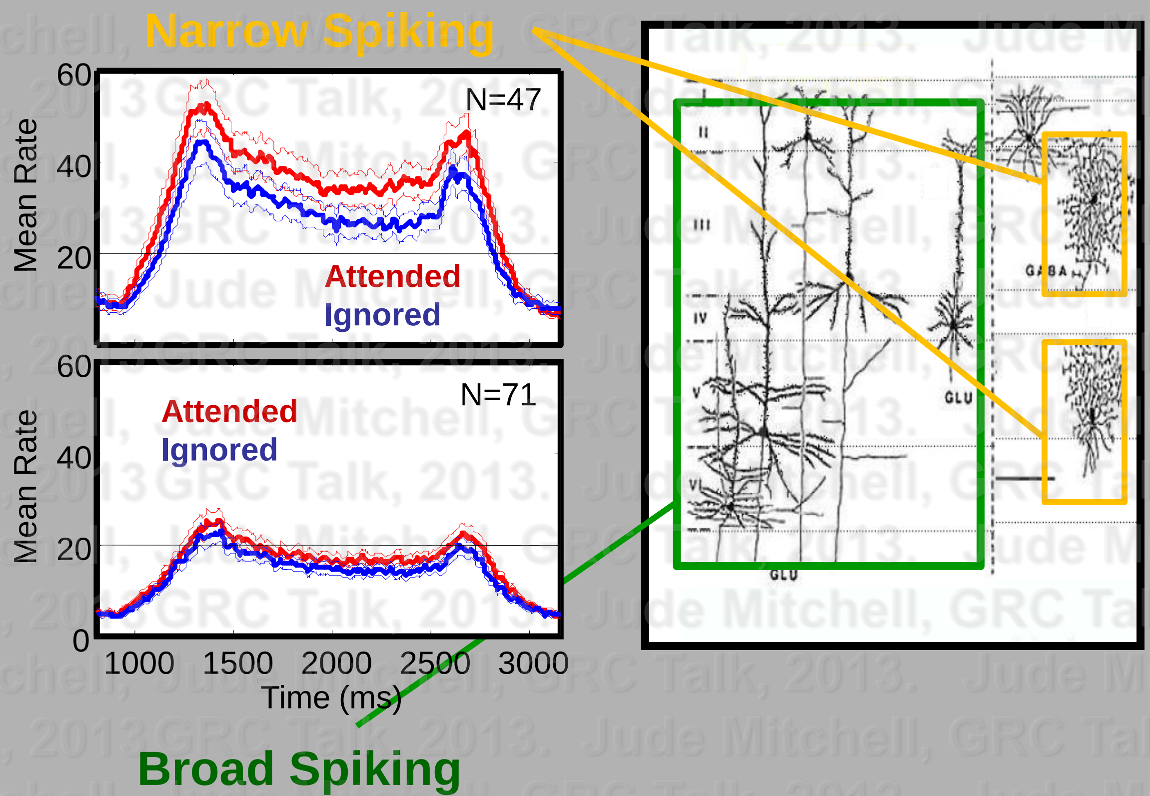

Recordings from macaque V4

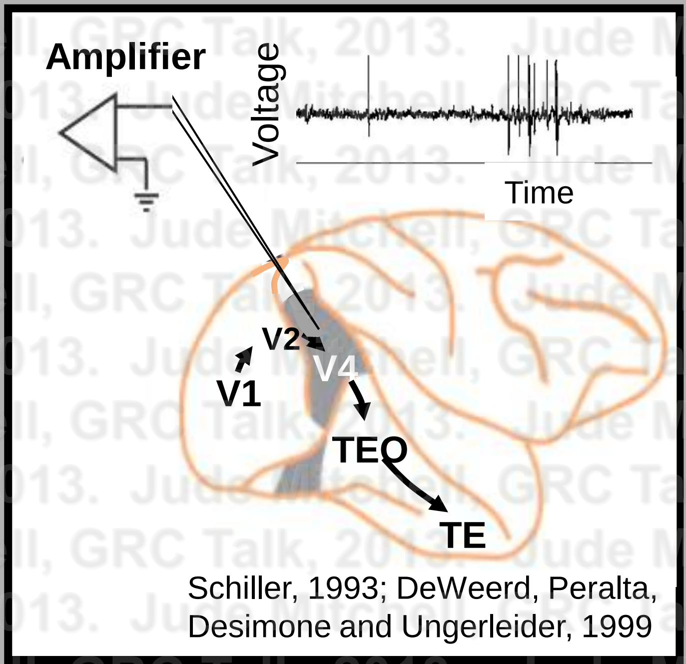


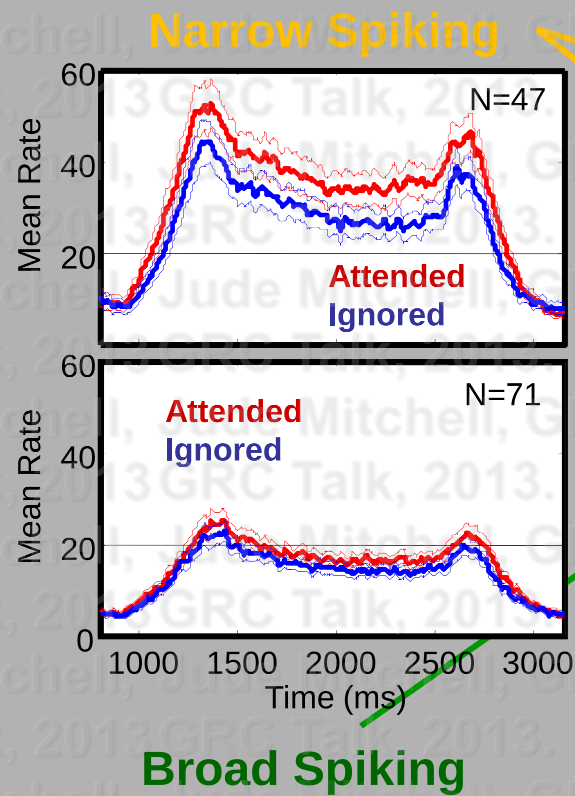


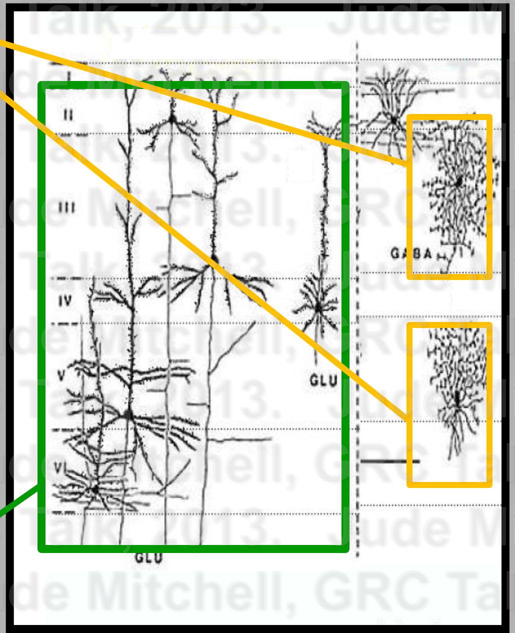

Recordings from macaque V4





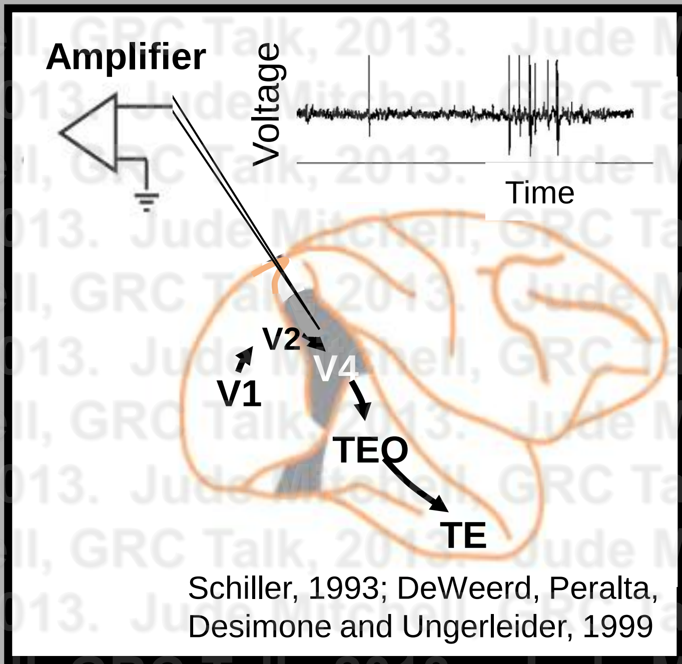

Recordings from macaque V4



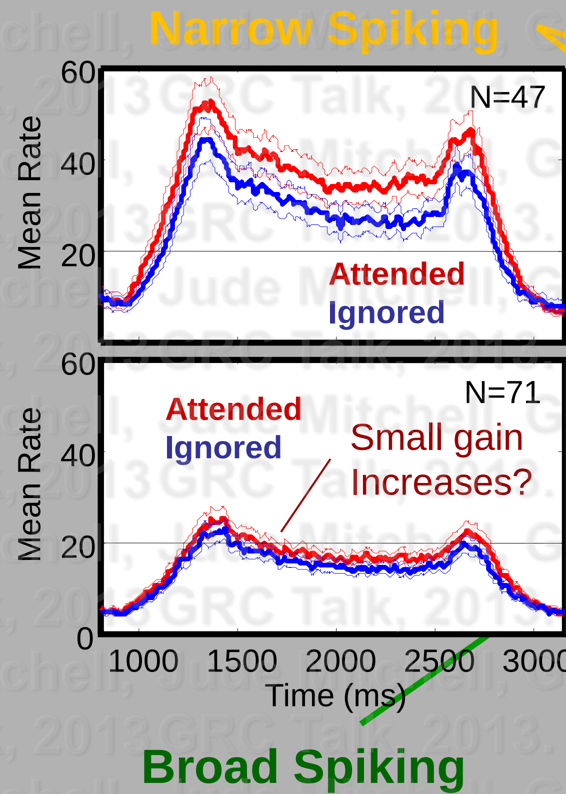



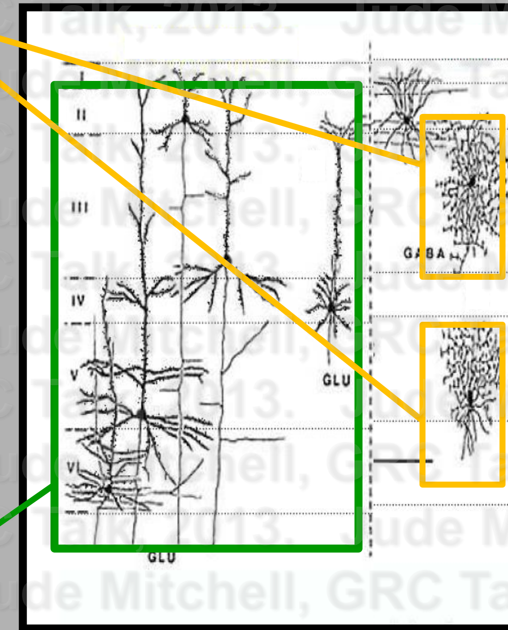

Attention increases local inhibition

**(Mitchell et al, Neuron 2007)**



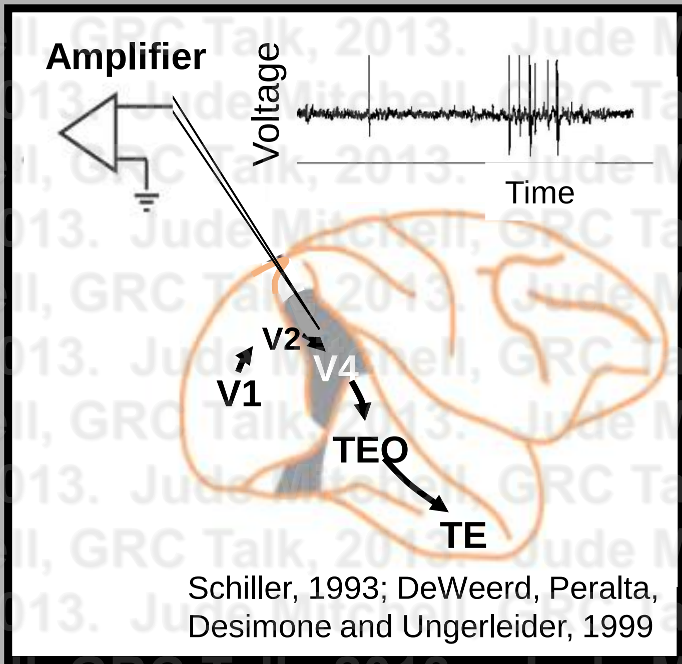

Recordings from macaque V4

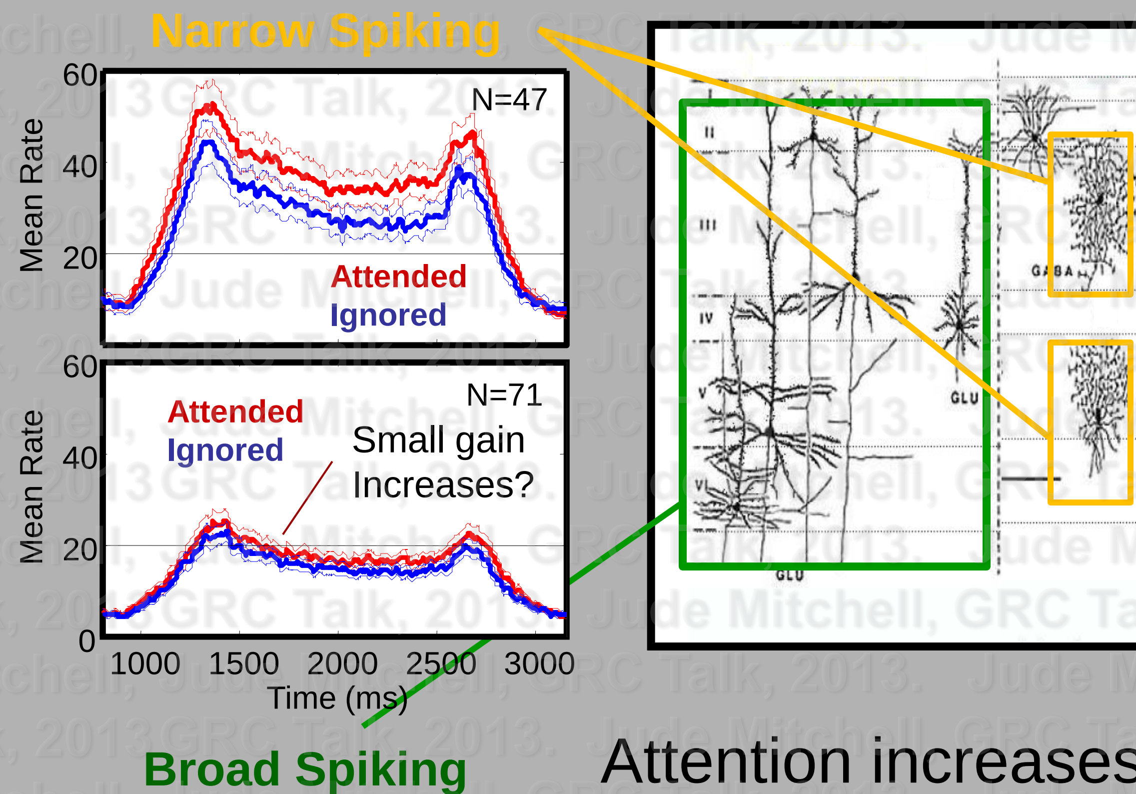


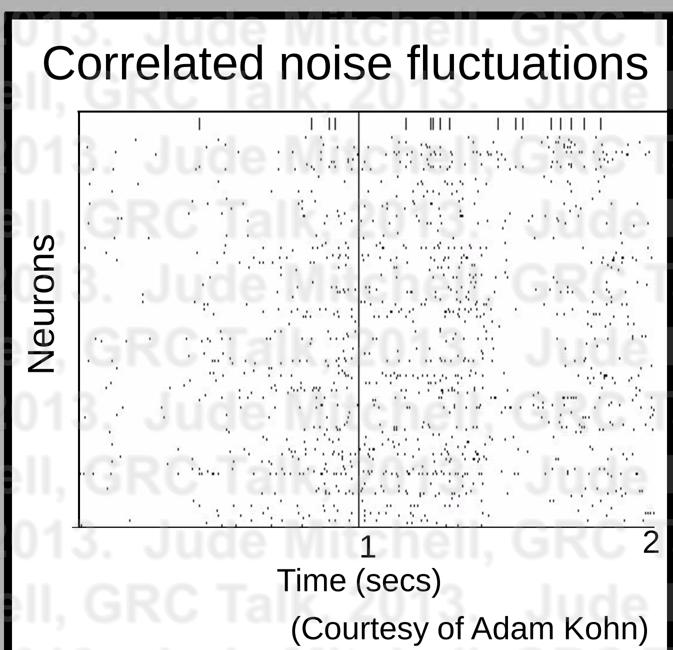




Attention increases local inhibition

**(Mitchell et al, Neuron 2007)**

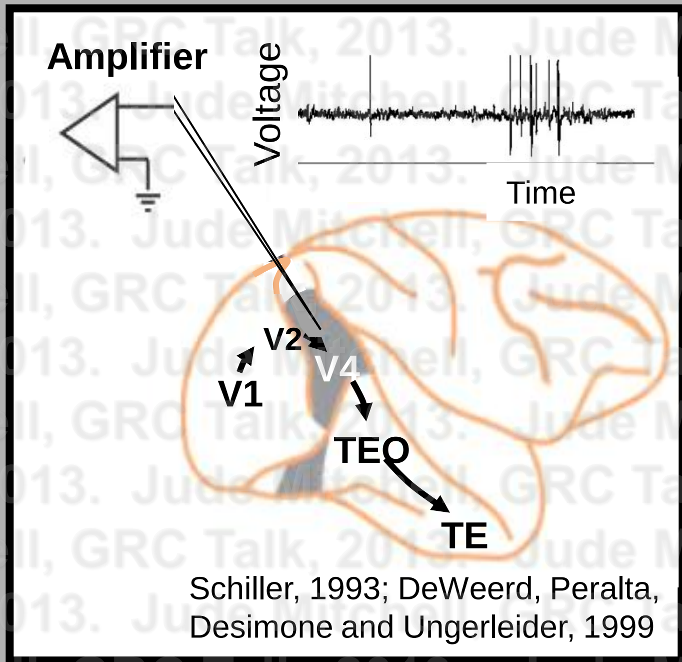


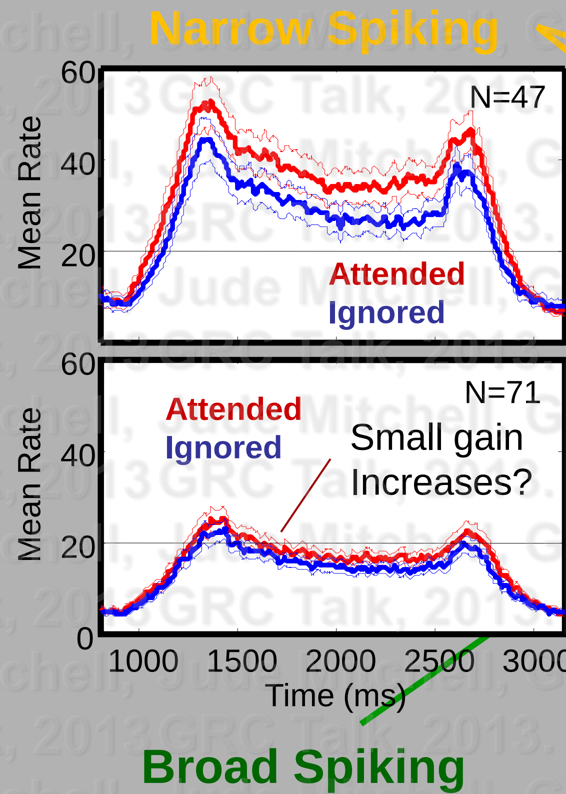



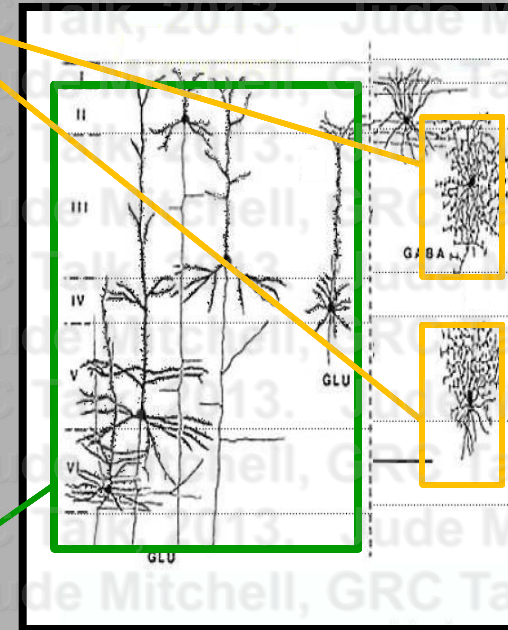




# Attention increases local inhibition

**(Mitchell et al, Neuron 2007)**

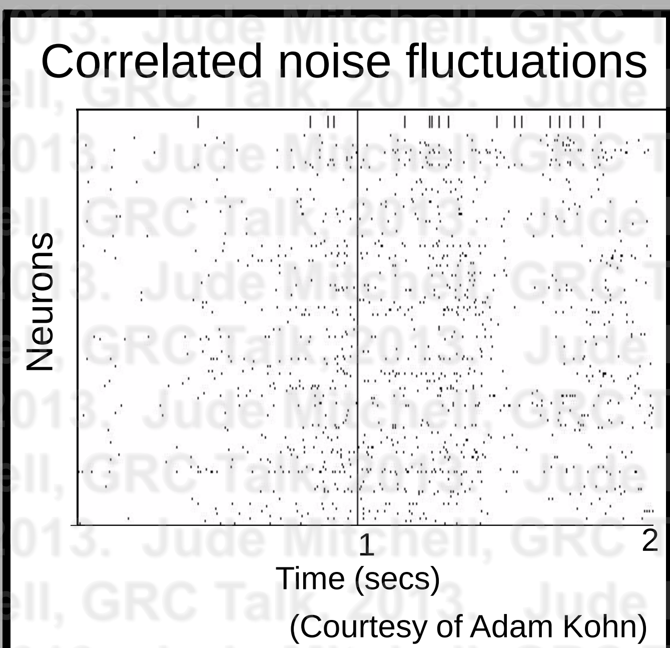


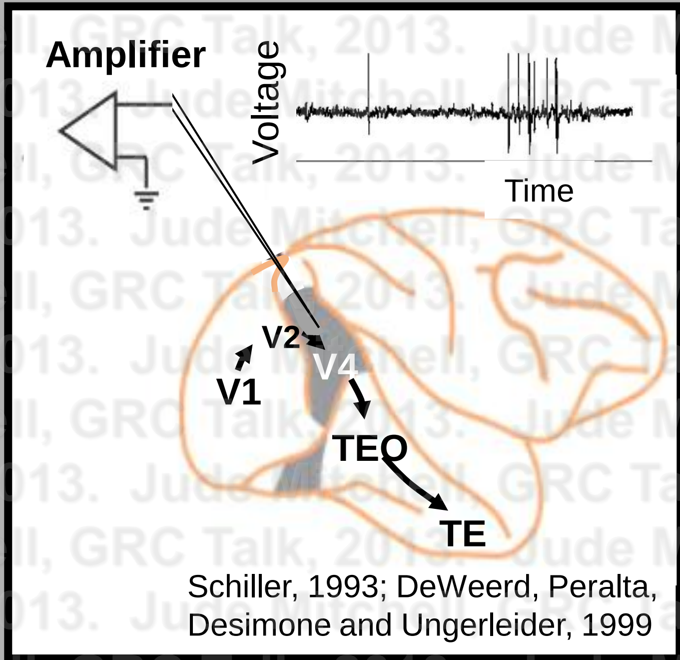



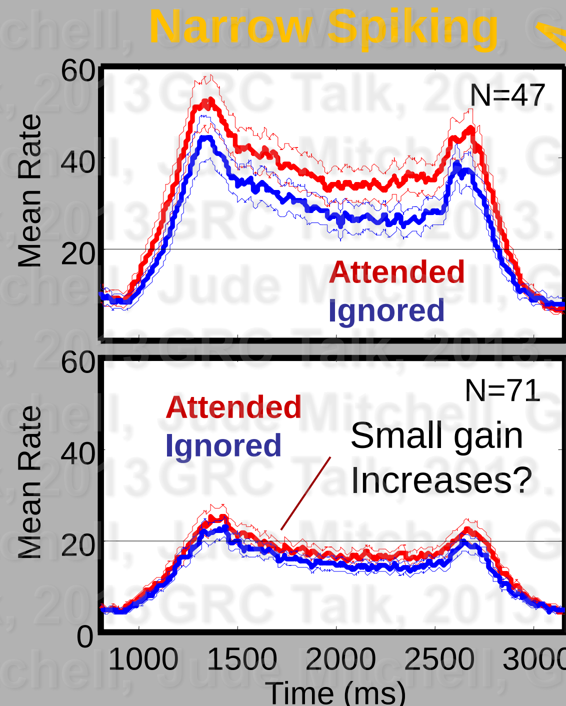



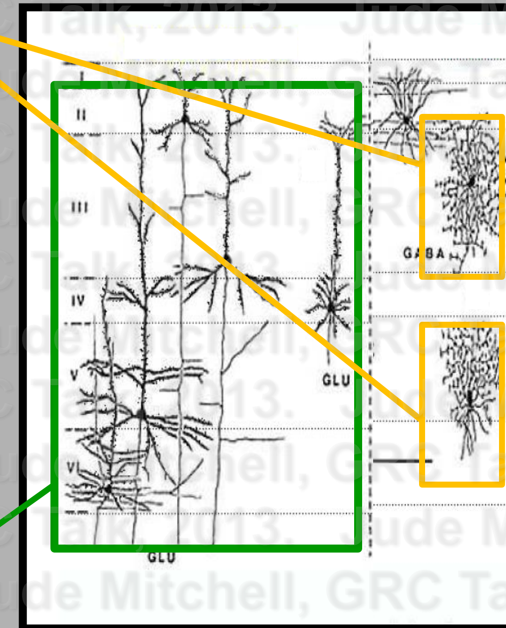

# Attention increases local inhibition

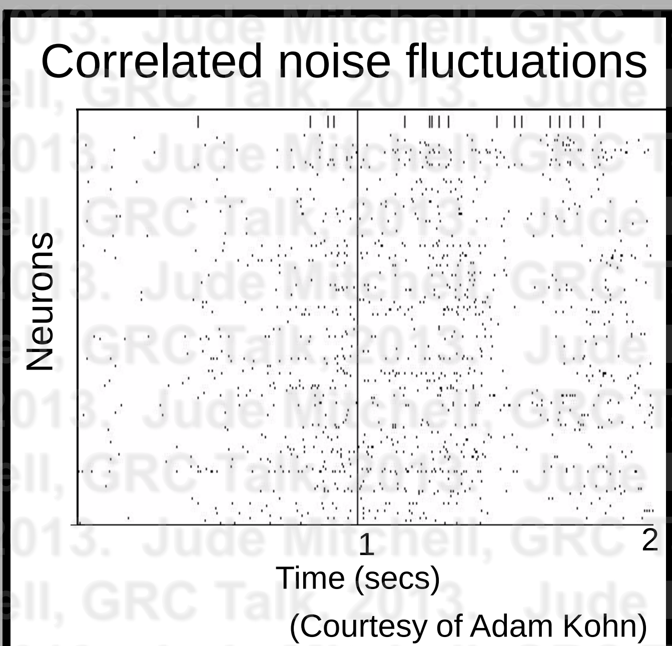
**(Mitchell et al, Neuron 2007)**

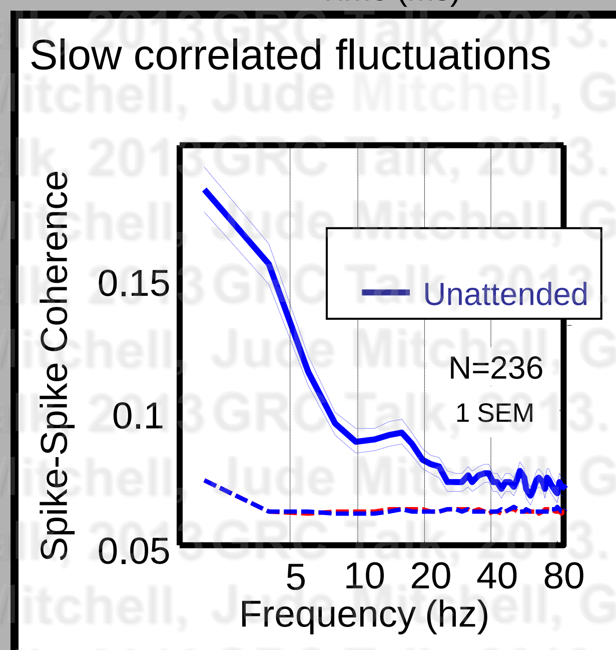




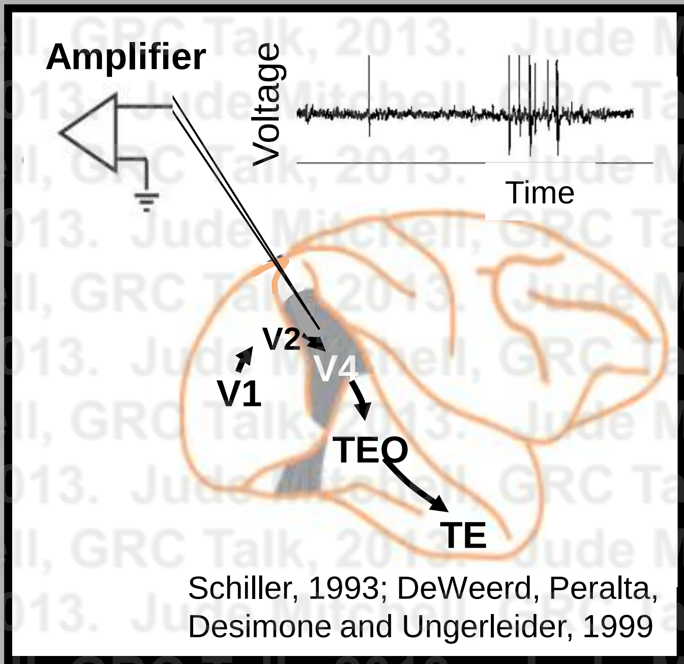



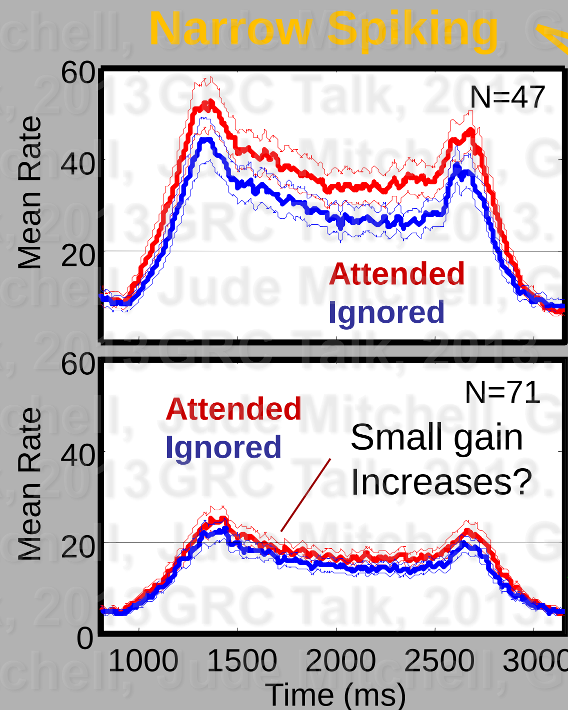



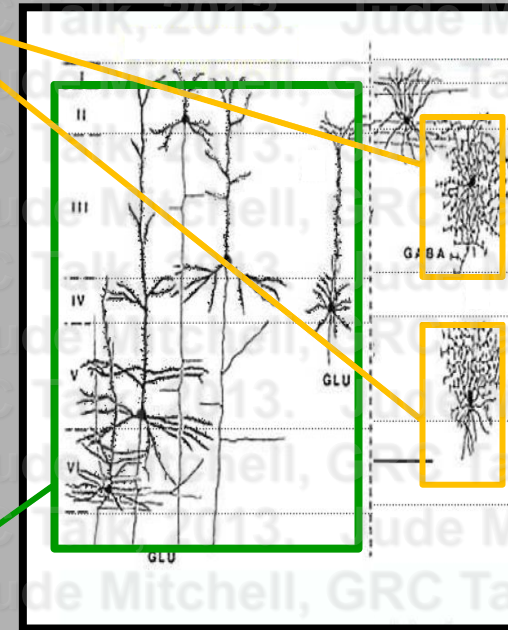



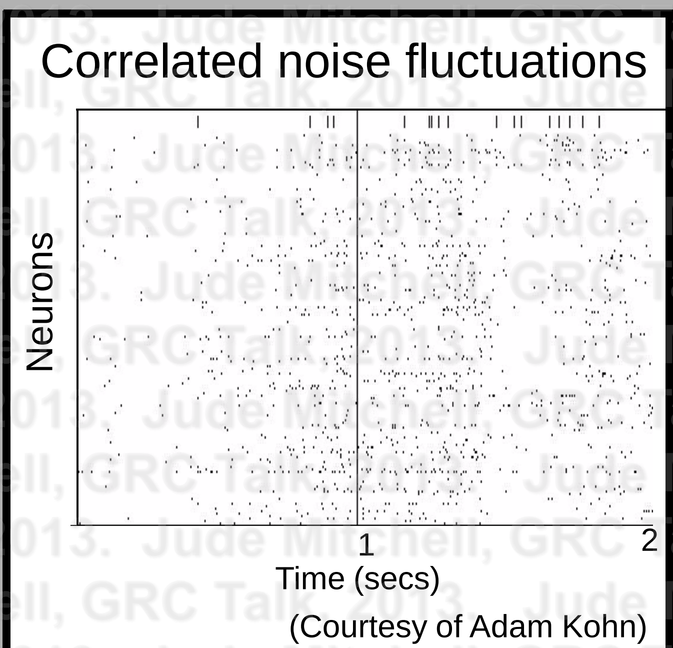

# Attention increases local inhibition

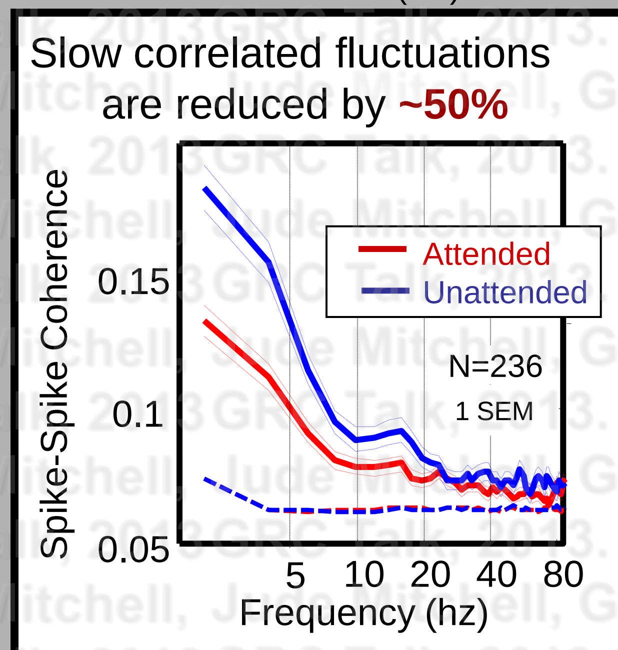
**(Mitchell et al, Neuron 2007)**



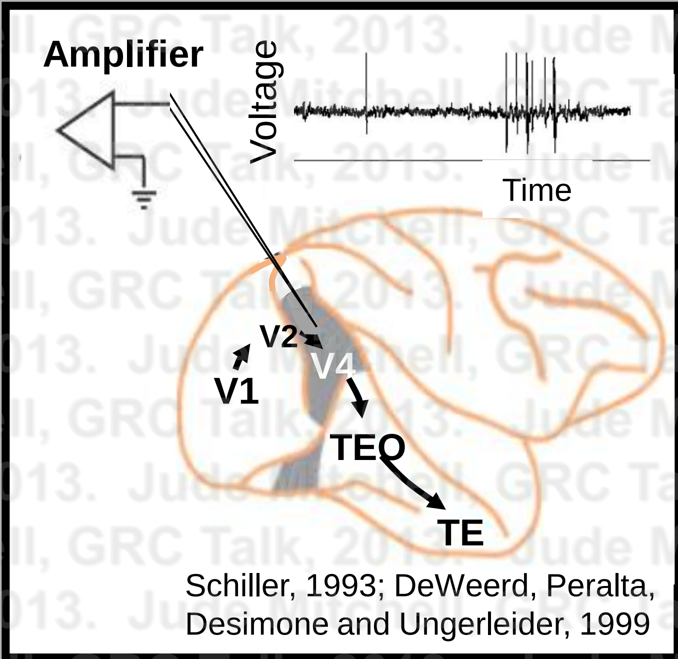



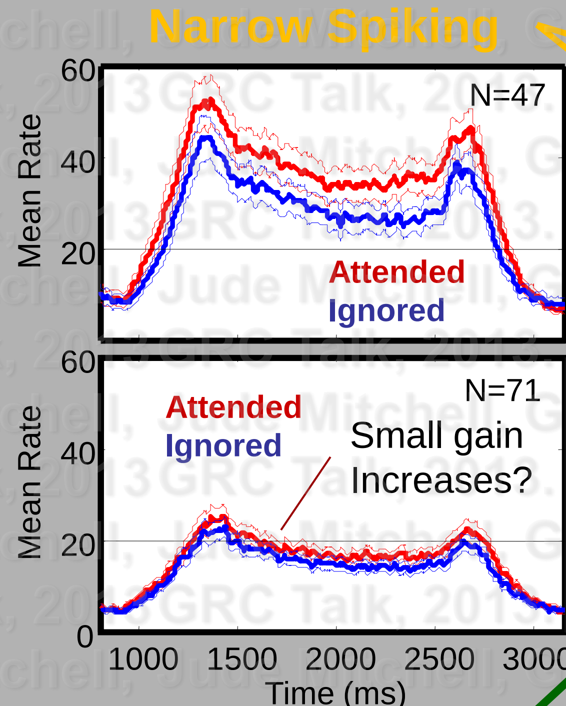



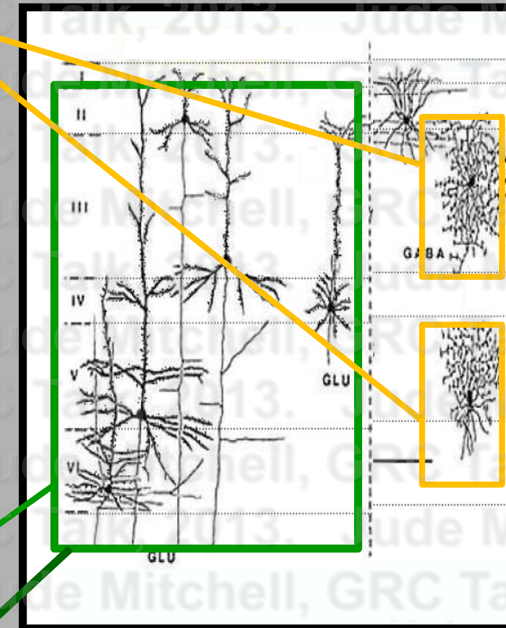



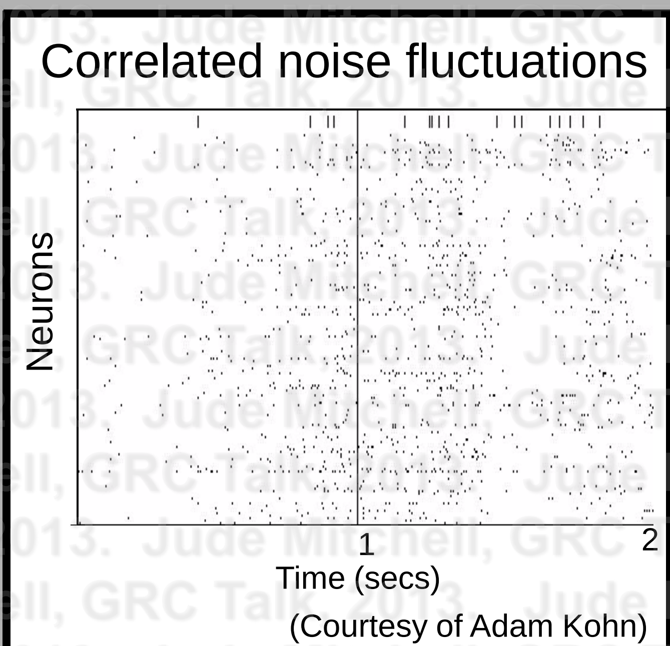

# Attention increases local inhibition

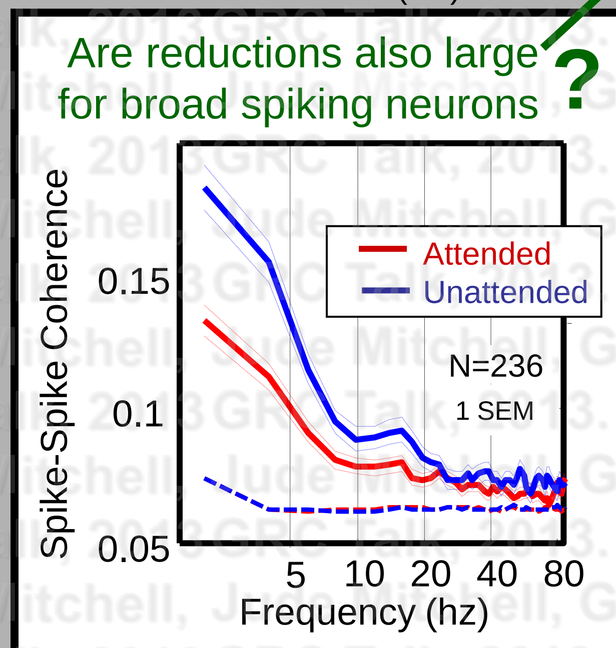
**(Mitchell et al, Neuron 2007)**



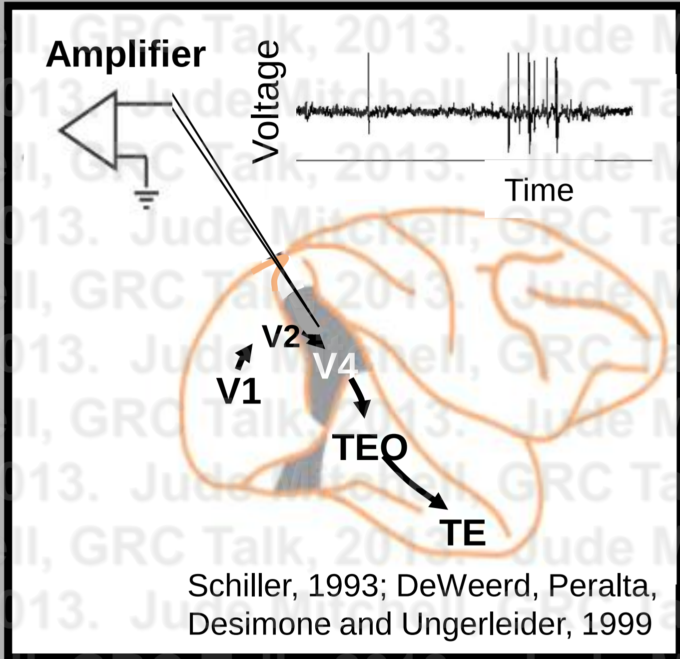



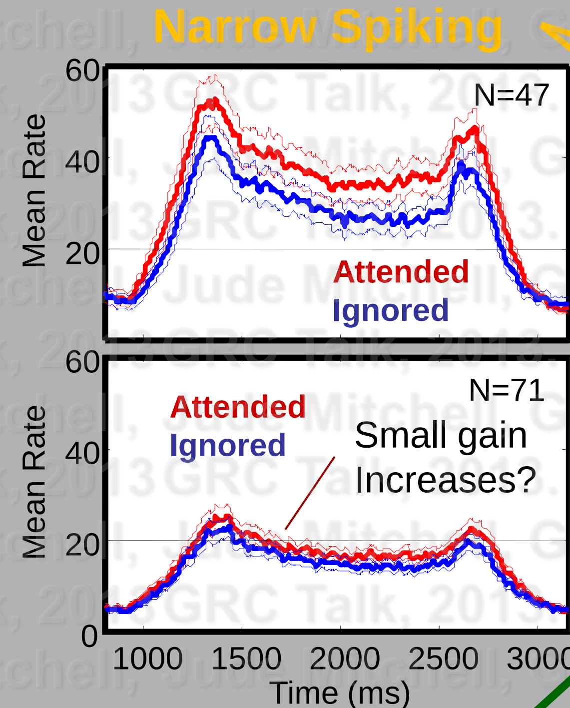



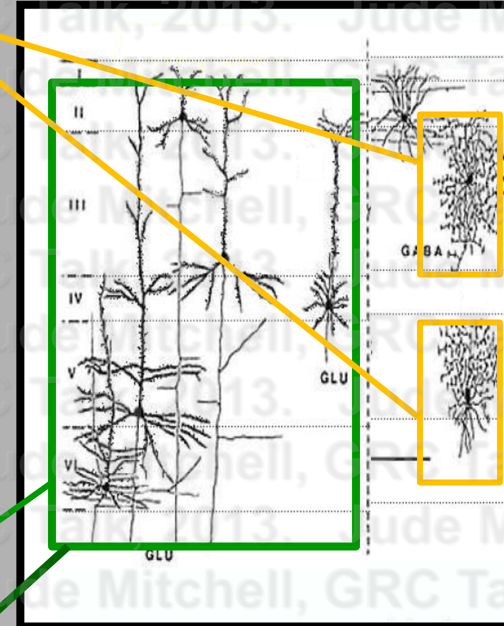



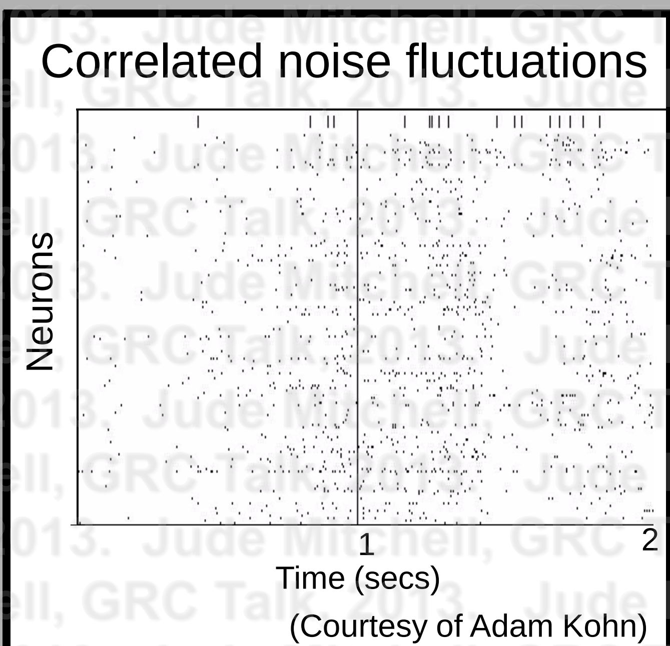

# Attention increases local inhibition

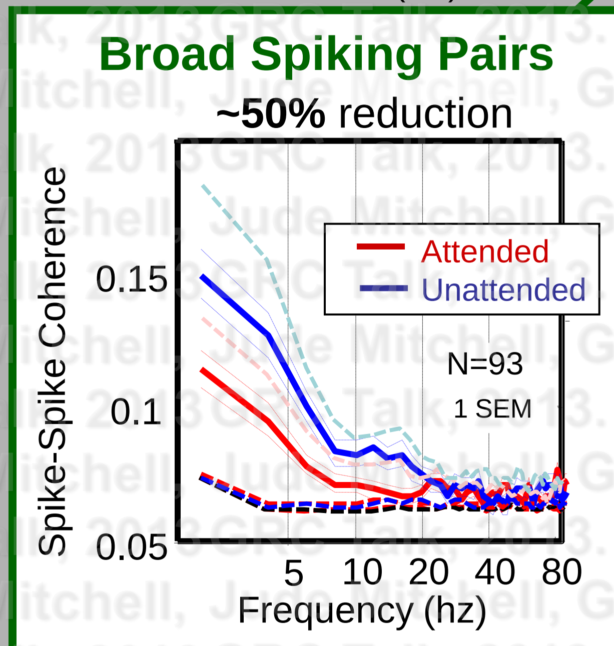
**(Mitchell et al, Neuron 2007)**



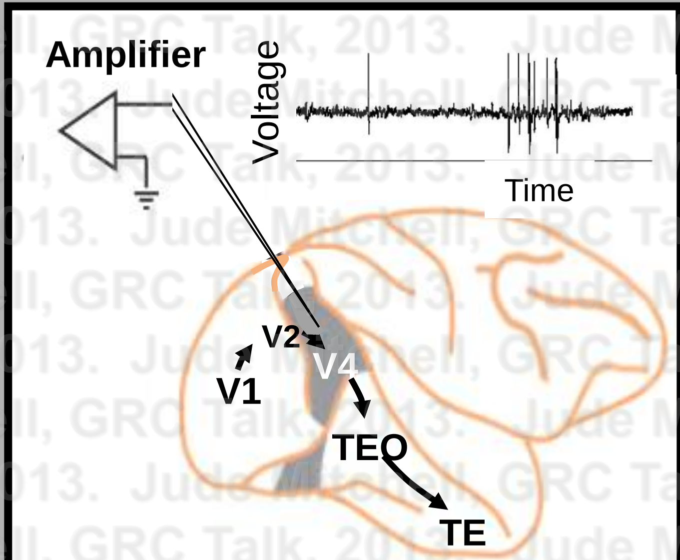



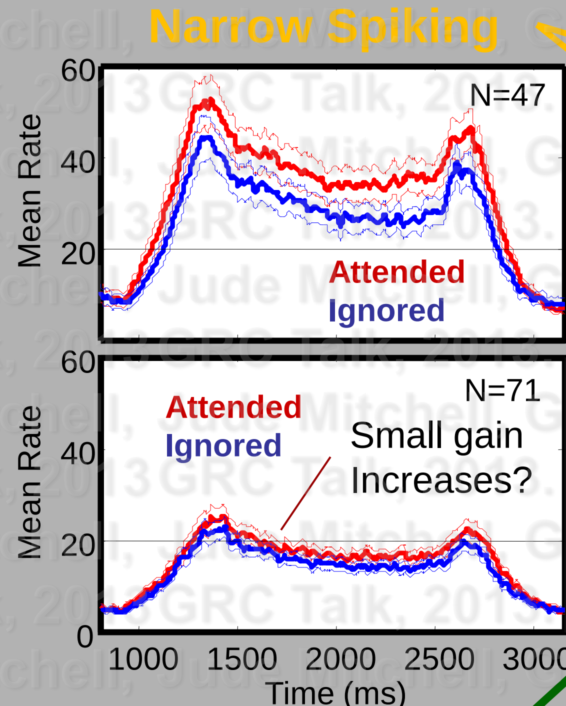



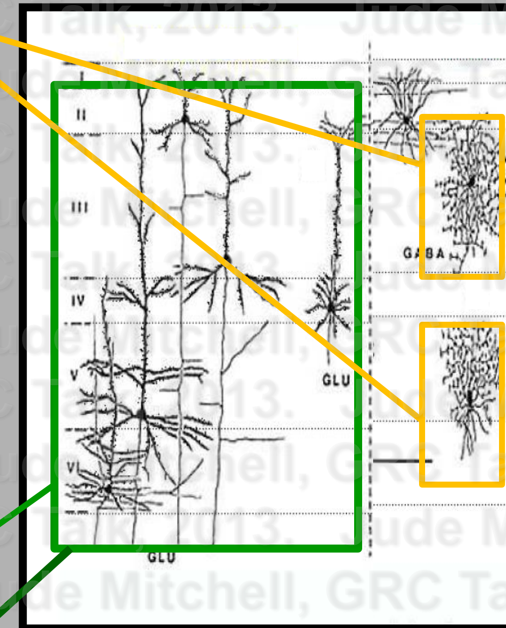

Attention increases local inhibition

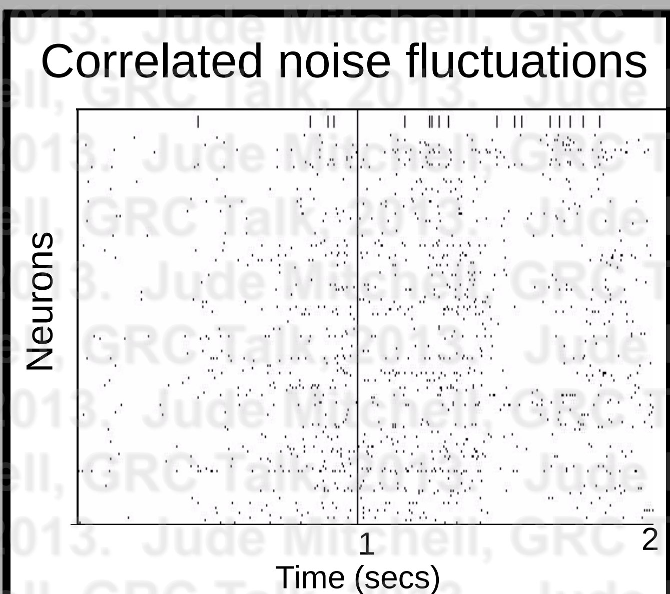
**(Mitchell et al, Neuron 2007)**



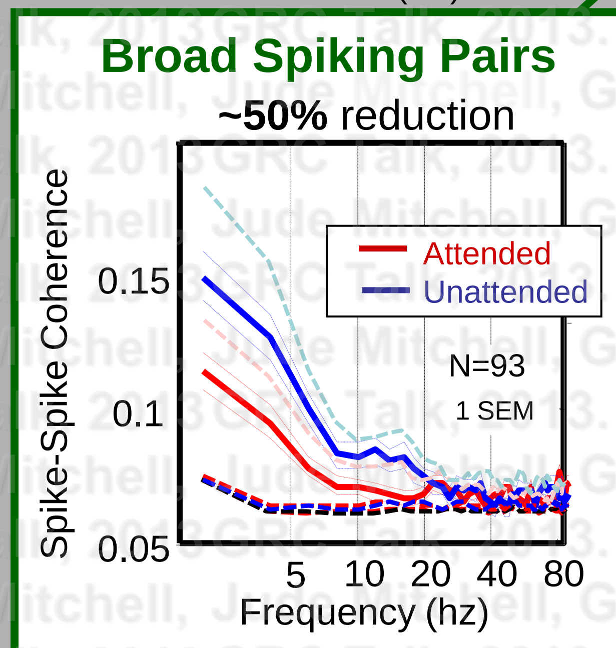

Schiller, 1993; DeWeerd, Peralta, Desimone and Ungerleider, 1999




(Courtesy of Adam Kohn)



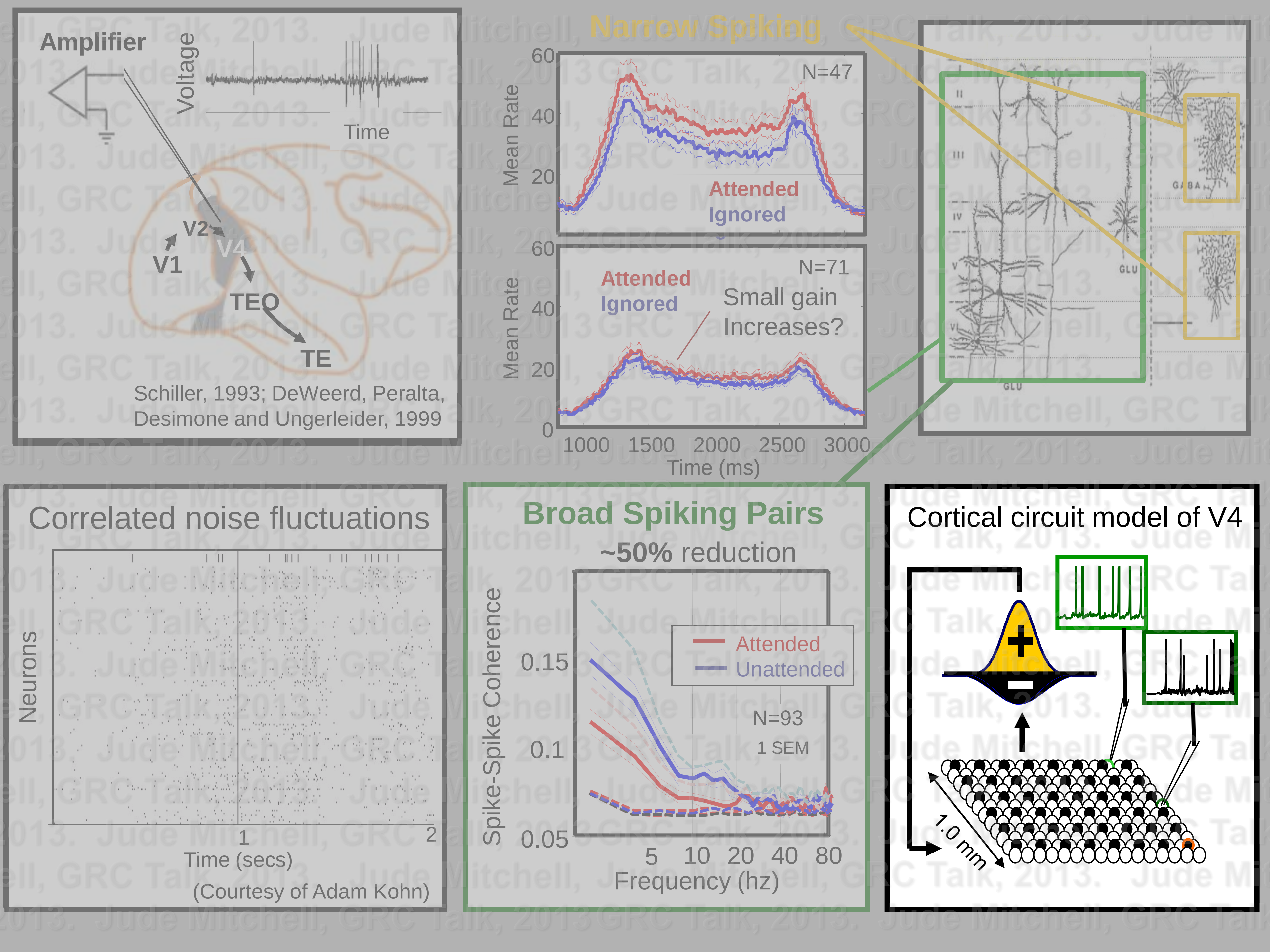

Attention increases local inhibition

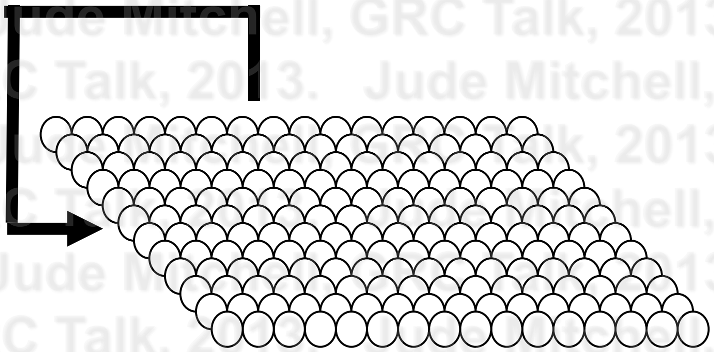
(Mitchell et al, Neuron 2007)

Attention reduces noise fluctuations

(Mitchell et al, Neuron 2009)

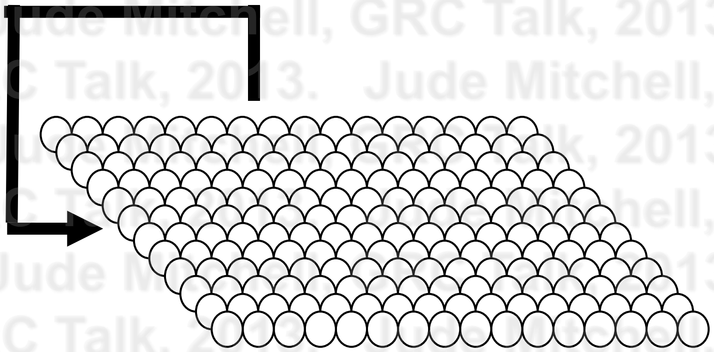
**Accounts for 80% signal improvement**


Amplifier
Voltage
Time
V1
V2
V4
TEO
TE
Schiller, 1993; DeWeerd, Peralta, Desimone and Ungerleider, 1999
Narrow Spiking
N=47
Attended
Ignored
N=71
Small gain Increases?
Mean Rate
60
40
20
0
1000 1500 2000 2500 3000
Time (ms)
II
III
IV
V
VI
GABA
GLU
Correlated noise fluctuations
Neurons
1
2
Time (secs)
(Courtesy of Adam Kohn)
Broad Spiking Pairs
~50% reduction
Spike-Spike Coherence
0.15
0.1
0.05
Attended
Unattended
N=93
1 SEM
5 10 20 40 80
Frequency (hz)
Cortical circuit model of V4
+
−
1.0 mm



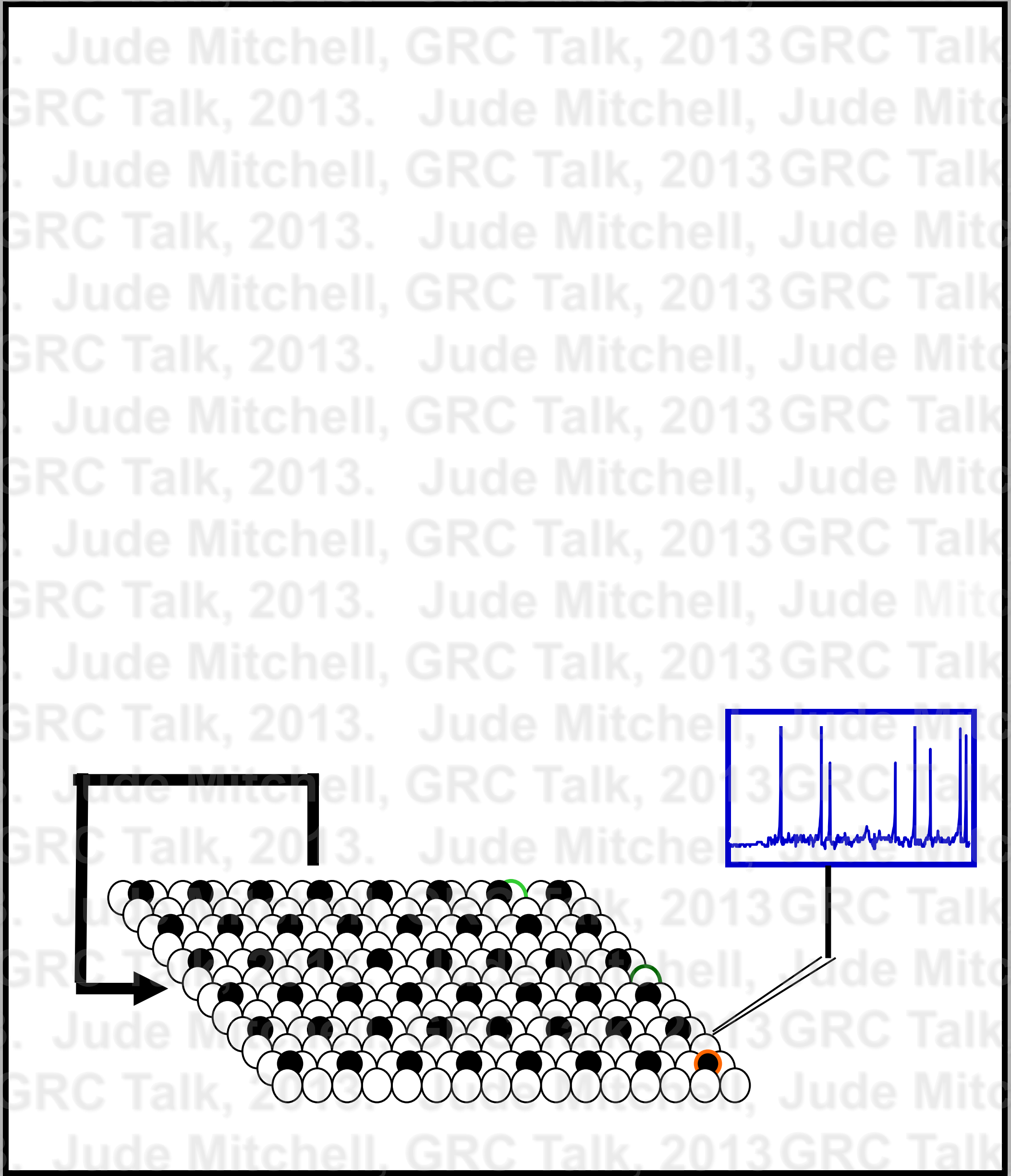
Shared variability
is intrinsic to
recurrent networks?

# Model architecture



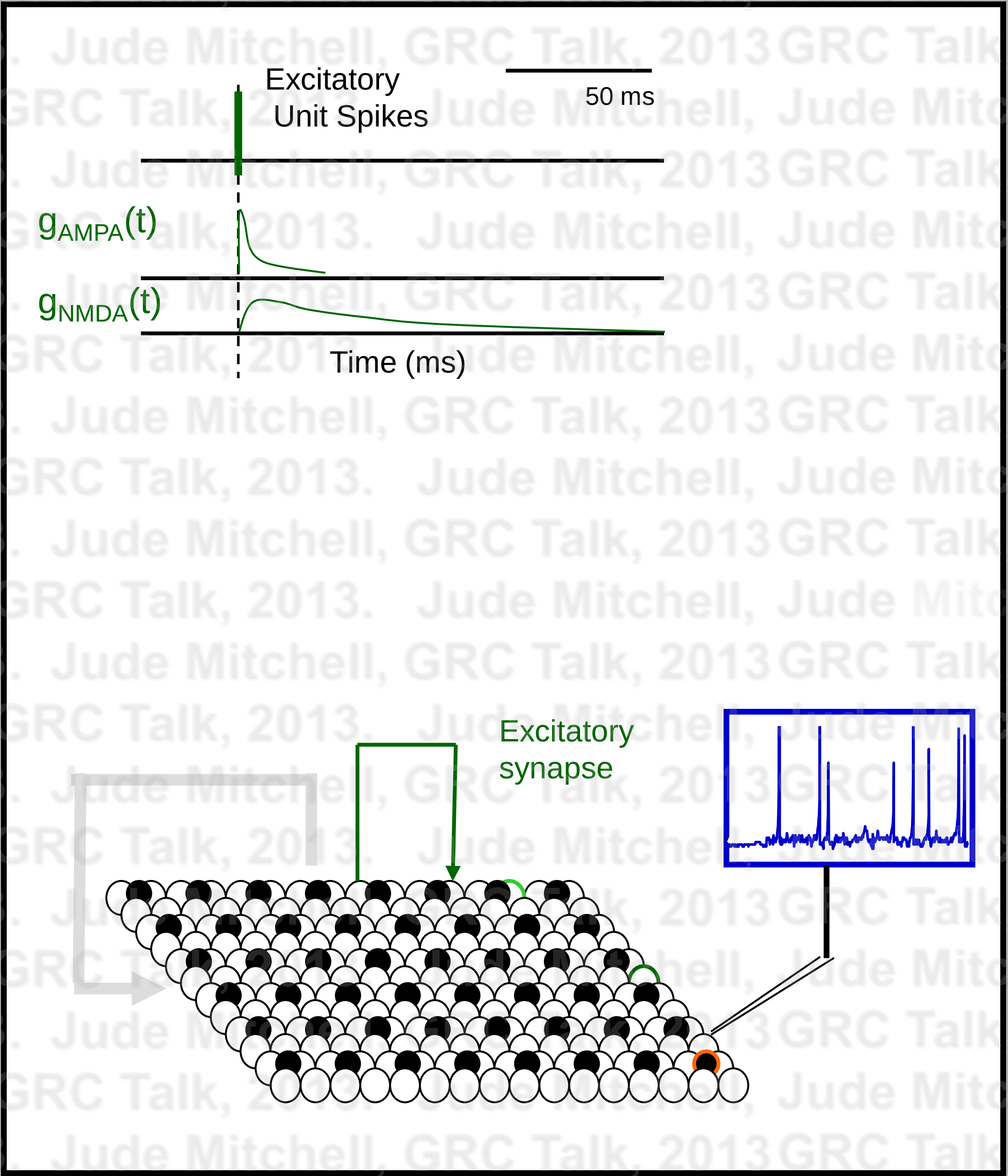
# Model architecture

2D grid of excitatory and inhibitory spiking units



# Model architecture

**2D grid of excitatory and Inhibitory spiking units**

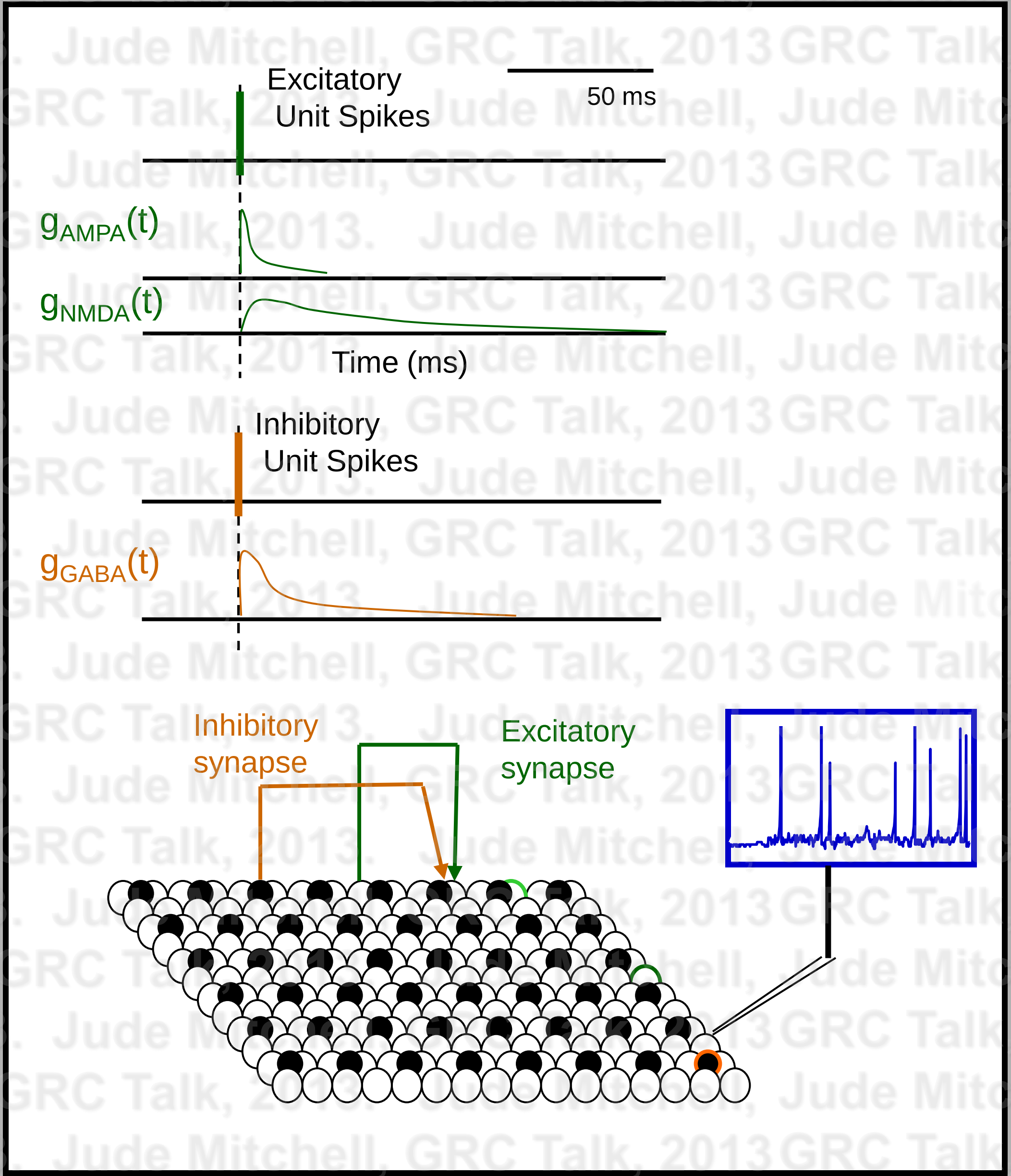



**Synaptic Conductances:**

$\tau_{AMPA}$ = 3 ms
$\tau_{NMDA}$ = 80 ms, $\tau_{rise}$ = 0.5 ms
$G_{NMDA}/G_{AMPA}$ = 0.45 (Myme et al, 2003)

# Model architecture

**2D grid of excitatory and Inhibitory spiking units**




**Synaptic Conductances:**

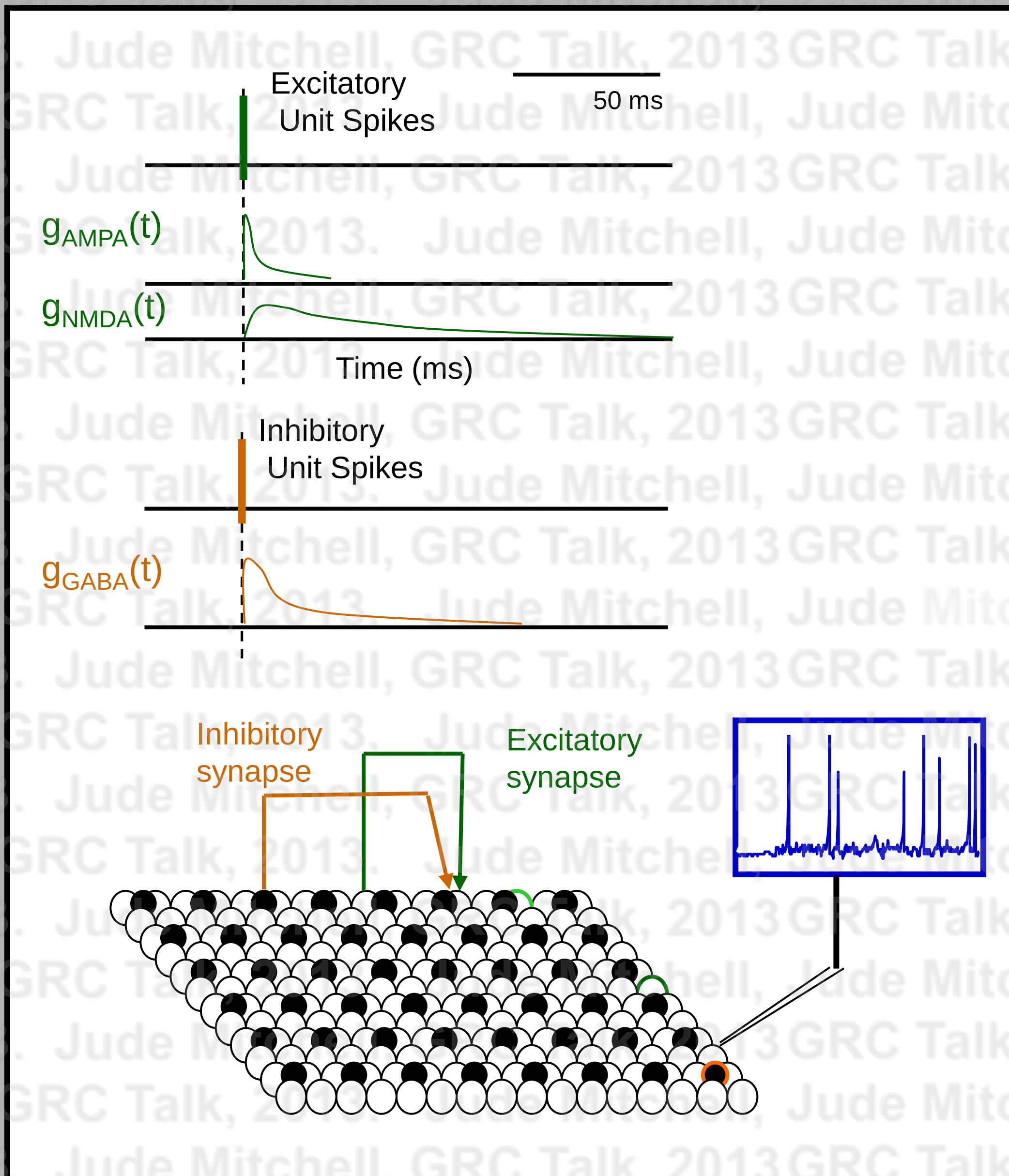
$\tau_{AMPA}$ = 3 ms

$\tau_{NMDA}$ = 80 ms, $\tau_{rise}$ = 0.5 ms

$G_{NMDA}/G_{AMPA}$ = 0.45 (Myme et al, 2003)

$\tau_{GABA}$ = 10 ms

# Model architecture




**2D grid of excitatory and Inhibitory spiking units**

**Synaptic Conductances:**

$\tau_{AMPA}$ = 3 ms

$\tau_{NMDA}$ = 80 ms, $\tau_{rise}$ = 0.5 ms

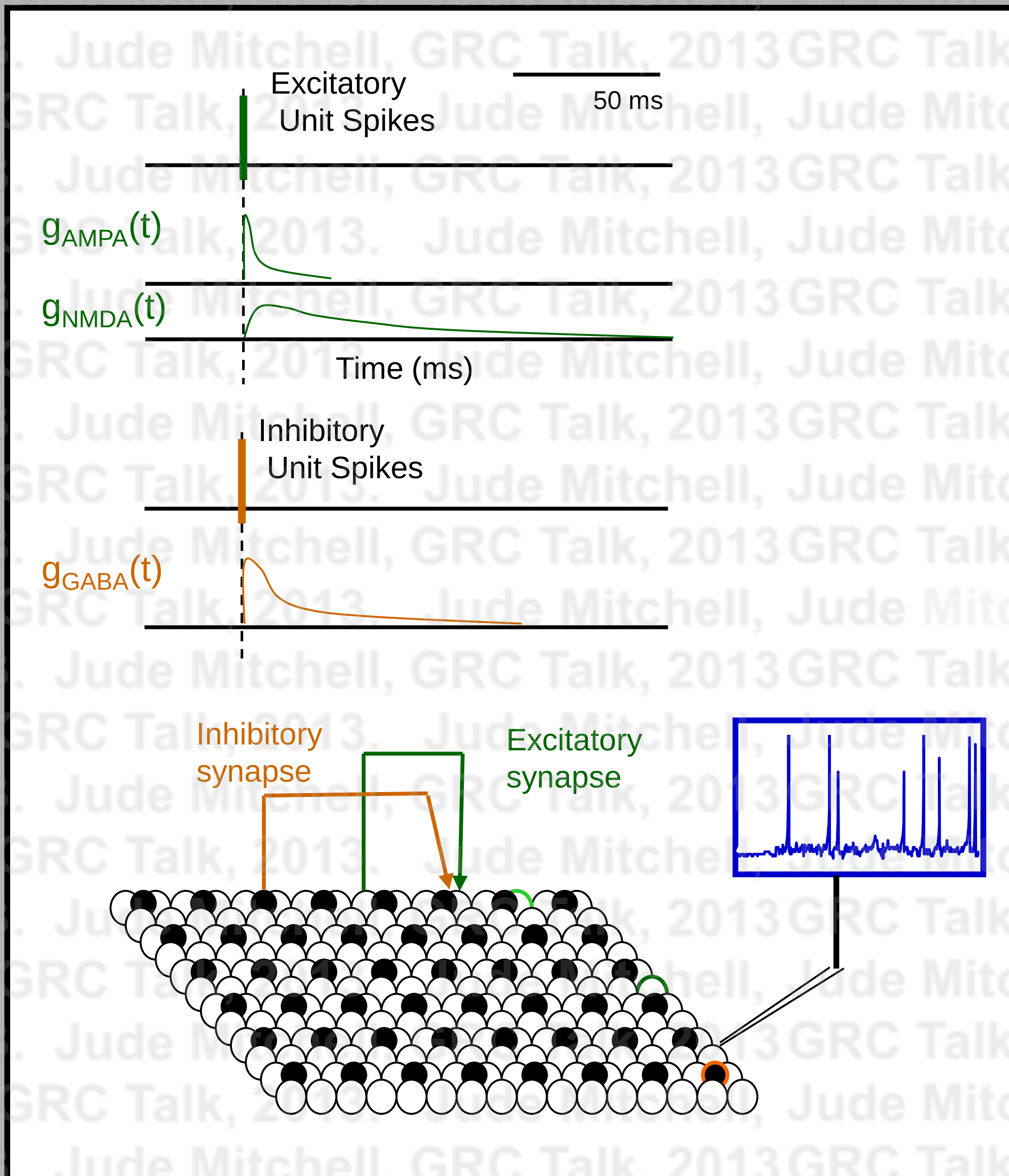
$G_{NMDA}/G_{AMPA}$ = 0.45 (Myme et al, 2003)

$\tau_{GABA}$ = 10 ms

**Net Synaptic Current:**

$$I_{syn} = \Sigma_i\, g_i^{AMPA}(t)\,(E_{AMPA}-v(t)) + \Sigma_j\, g_j^{NMDA}(t)\,(E_{NMDA}-v(t)) + \Sigma_k\, g_k^{GABA}(t)\,(E_{GABA}-v(t))$$

# Model architecture




**2D grid of excitatory and Inhibitory spiking units**

**Synaptic Conductances:**

$\tau_{AMPA}$ = 3 ms

$\tau_{NMDA}$ = 80 ms, $\tau_{rise}$ = 0.5 ms

$G_{NMDA}/G_{AMPA}$ = 0.45 (Myme et al, 2003)

$\tau_{GABA}$ = 10 ms

**Net Synaptic Current:**

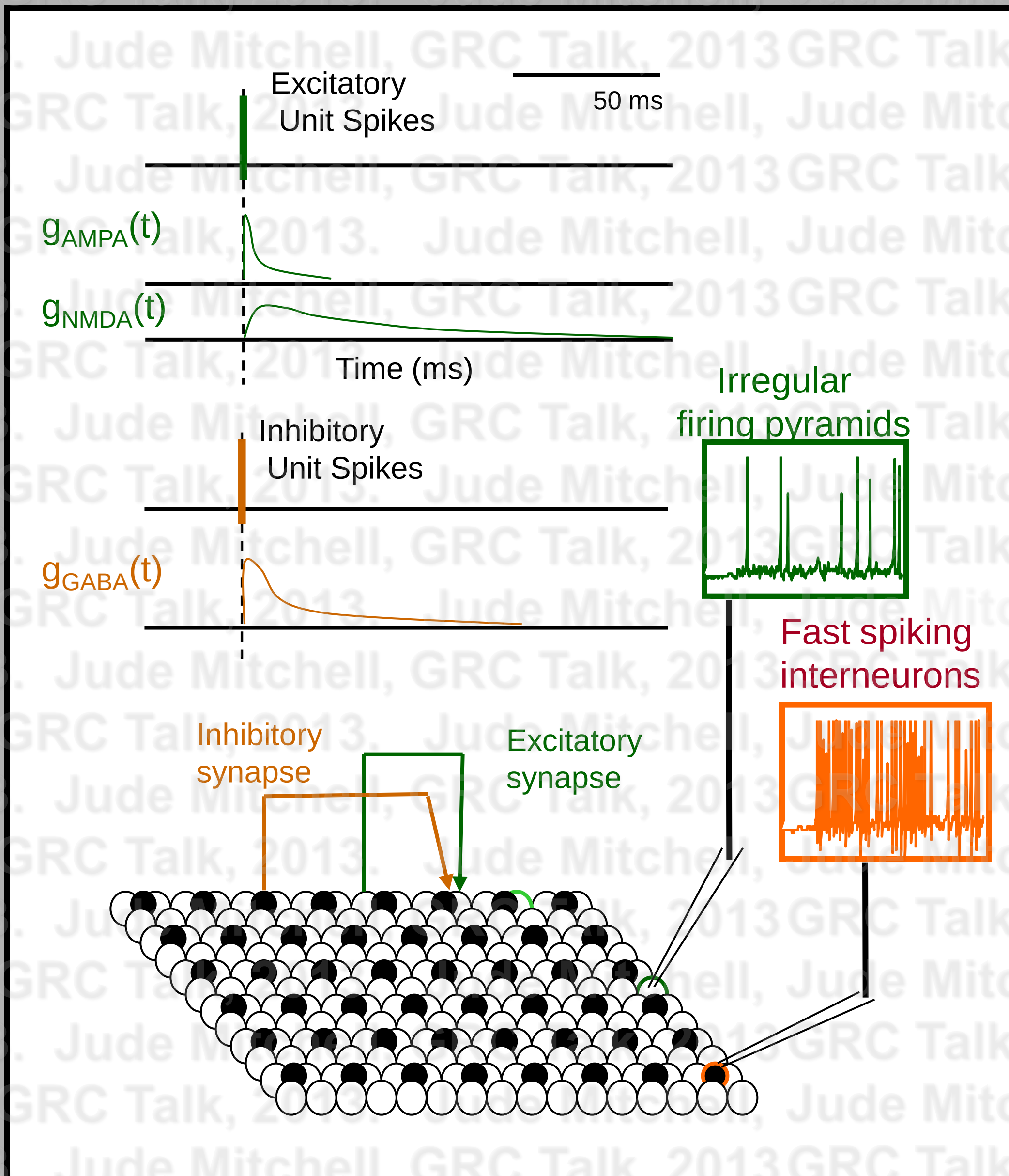
$$I_{syn} = \Sigma_i\, g_i^{AMPA}(t)\ (E_{AMPA} - v(t)) + \Sigma_j\, g_j^{NMDA}(t)\ (E_{NMDA} - v(t)) + \Sigma_k\, g_k^{GABA}(t)\ (E_{GABA} - v(t))$$

**Integrate and Fire**

$$\tau\, dv/dt = \mathbf{I_{syn}}$$

if (v > threshold) spike, v -> c

# Model architecture




**2D grid of excitatory and Inhibitory spiking units**

**Synaptic Conductances:**

$\tau_{AMPA}$ = 3 ms
$\tau_{NMDA}$ = 80 ms, $\tau_{rise}$ = 0.5 ms
$G_{NMDA}/G_{AMPA}$ = 0.45 (Myme et al, 2003)
$\tau_{GABA}$ = 10 ms

**Net Synaptic Current:**

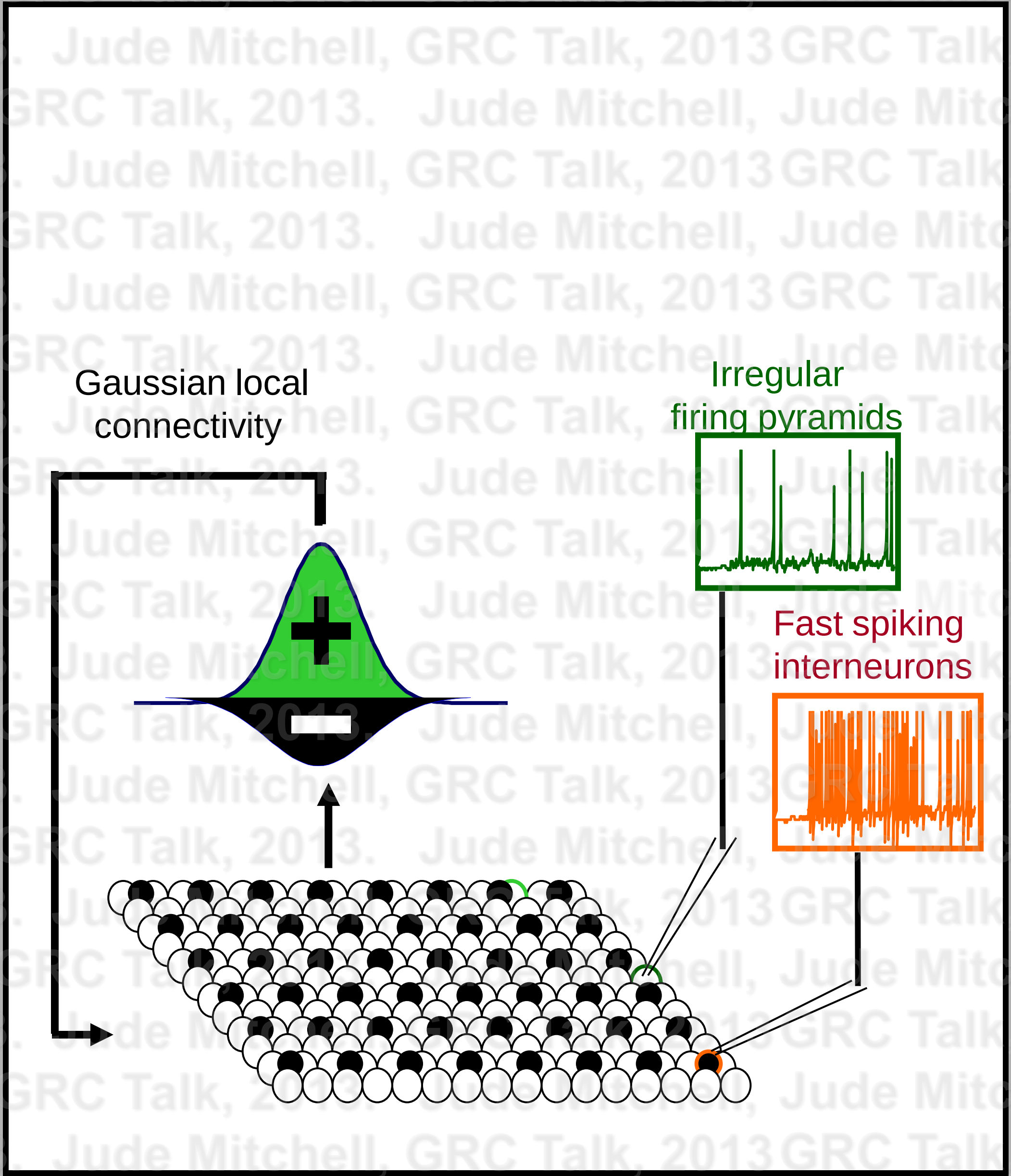
$$I_{syn} = \Sigma_i\, g_i^{AMPA}(t)\,(E_{AMPA}-v(t)) + \Sigma_j\, g_j^{NMDA}(t)\,(E_{NMDA}-v(t)) + \Sigma_k\, g_k^{GABA}(t)\,(E_{GABA}-v(t))$$

**Integrate and Fire Izhikevich Neurons(2003):**

$\tau\, dv/dt = \mathbf{I_{syn}}$

if (v > threshold) spike, v -> c

# Model architecture




**2D grid of excitatory and Inhibitory spiking units**

**Synaptic Conductances:**

$\tau_{AMPA}$ = 3 ms

$\tau_{NMDA}$ = 80 ms, $\tau_{rise}$ = 0.5 ms

$G_{NMDA}/G_{AMPA}$ = 0.45 (Myme et al, 2003)

$\tau_{GABA}$ = 10 ms

**Net Synaptic Current:**

$$I_{syn} = \Sigma_i\, g_i^{AMPA}(t)\ (E_{AMPA}-v(t)) + \Sigma_j\, g_j^{NMDA}(t)\ (E_{NMDA}-v(t)) + \Sigma_k\, g_k^{GABA}(t)\ (E_{GABA}-v(t))$$

**Integrate and Fire Izhikevich Neurons(2003):**

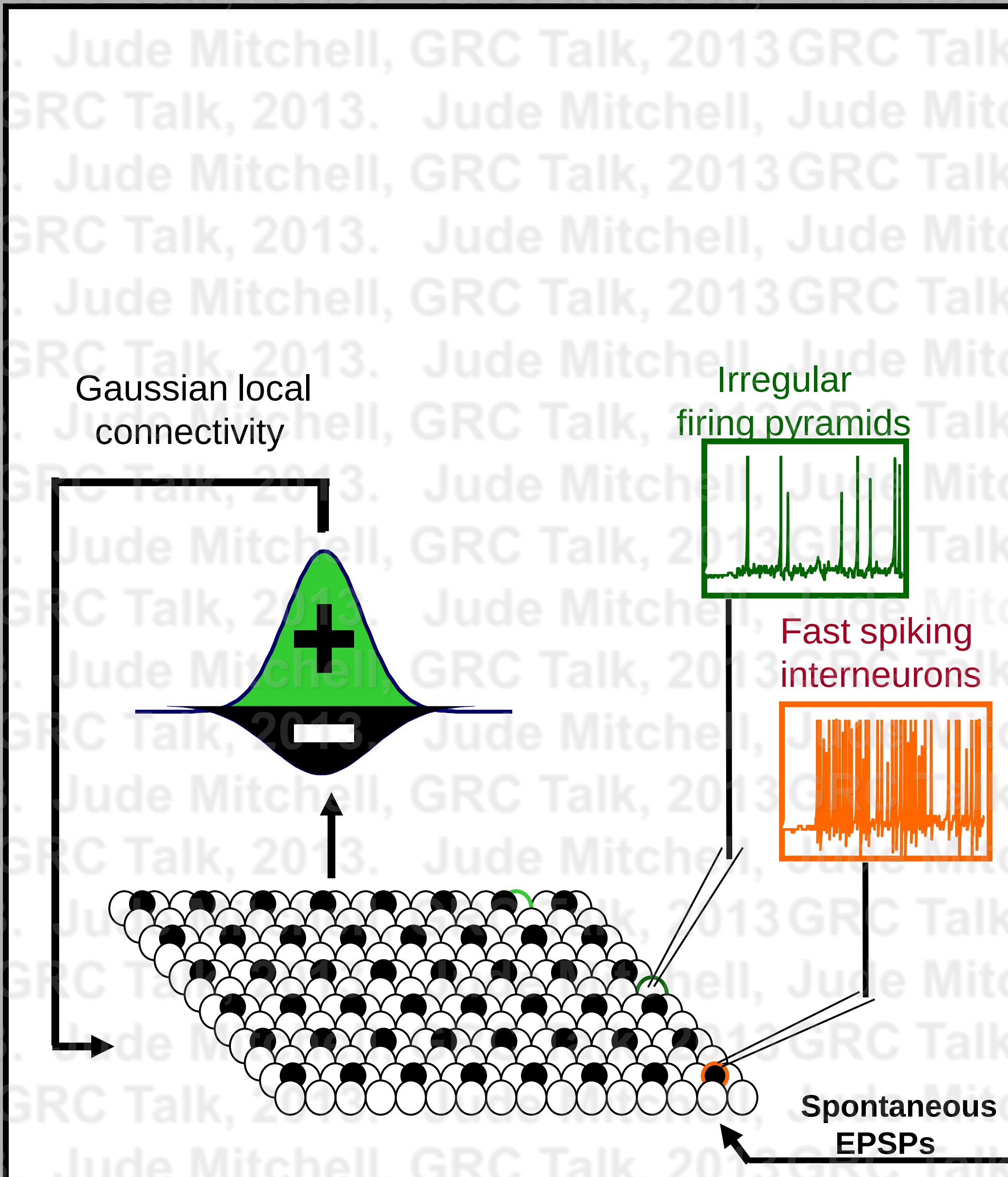
$\tau\, dv/dt = \mathbf{I_{syn}}$

if (v > threshold) spike, v -> c

**Connectivity:**

Shift-invariant 2D Gaussian weights for excitatory and inhibitory connections

# Model architecture




**2D grid of excitatory and Inhibitory spiking units**

**Synaptic Conductances:**

$\tau_{AMPA}$ = 3 ms
$\tau_{NMDA}$ = 80 ms, $\tau_{rise}$ = 0.5 ms
$G_{NMDA}/G_{AMPA}$ = 0.45 (Myme et al, 2003)
$\tau_{GABA}$ = 10 ms

**Net Synaptic Current:**

$$I_{syn} = \Sigma_i\, g_i^{AMPA}(t)\ (E_{AMPA}-v(t)) + \Sigma_j\, g_j^{NMDA}(t)\ (E_{NMDA}-v(t)) + \Sigma_k\, g_k^{GABA}(t)\ (E_{GABA}-v(t))$$

**Integrate and Fire Izhikevich Neurons(2003):**

$\tau\, dv/dt = \mathbf{I_{syn}}$

if (v > threshold) spike, v -> c

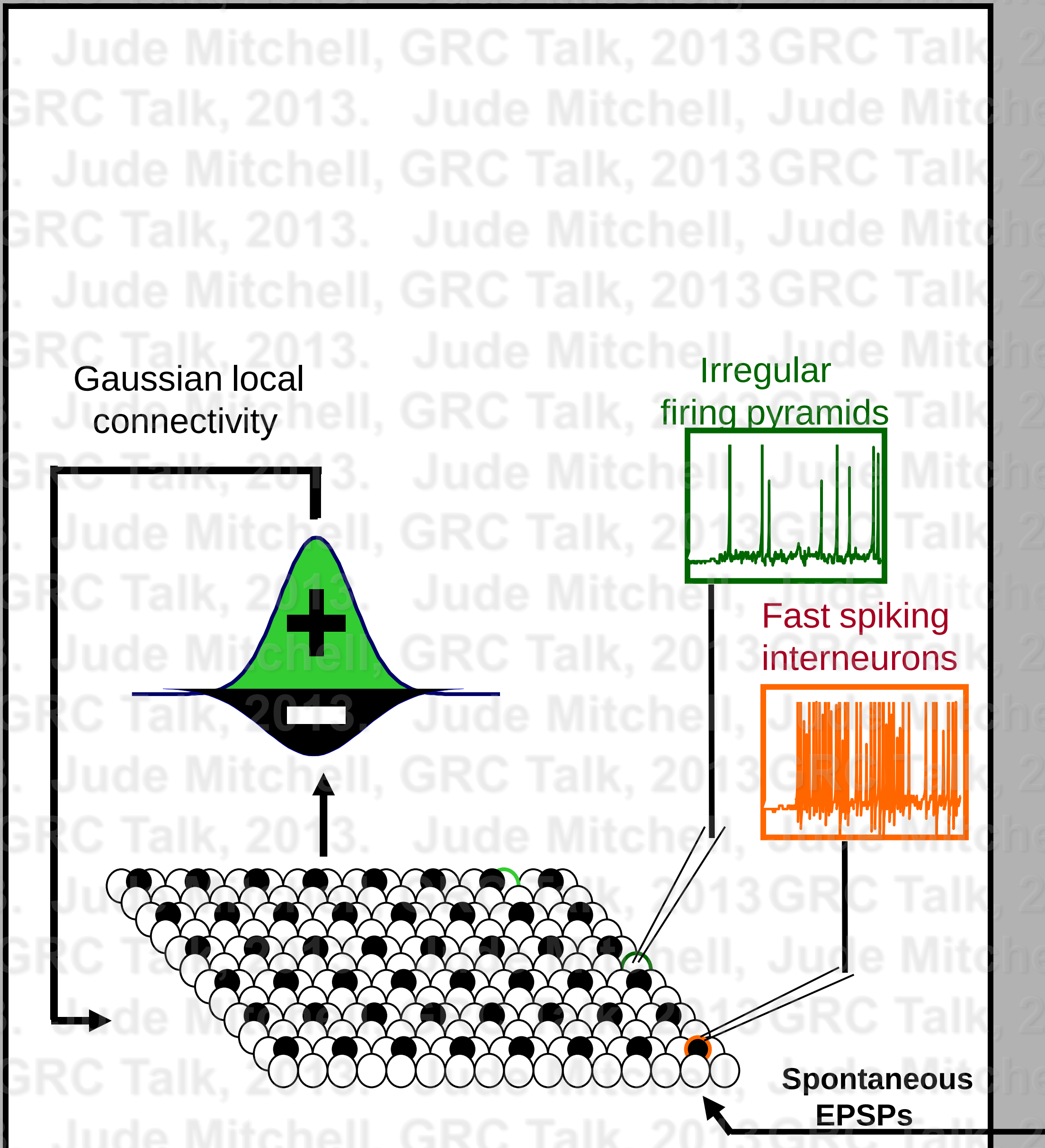
**Connectivity:**

Shift-invariant 2D Gaussian weights for excitatory and inhibitory connections

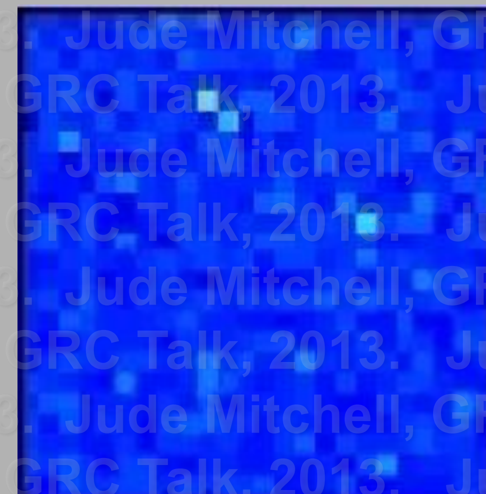
**Background:**

Independent Poisson events on excitatory and inhibitory synapses

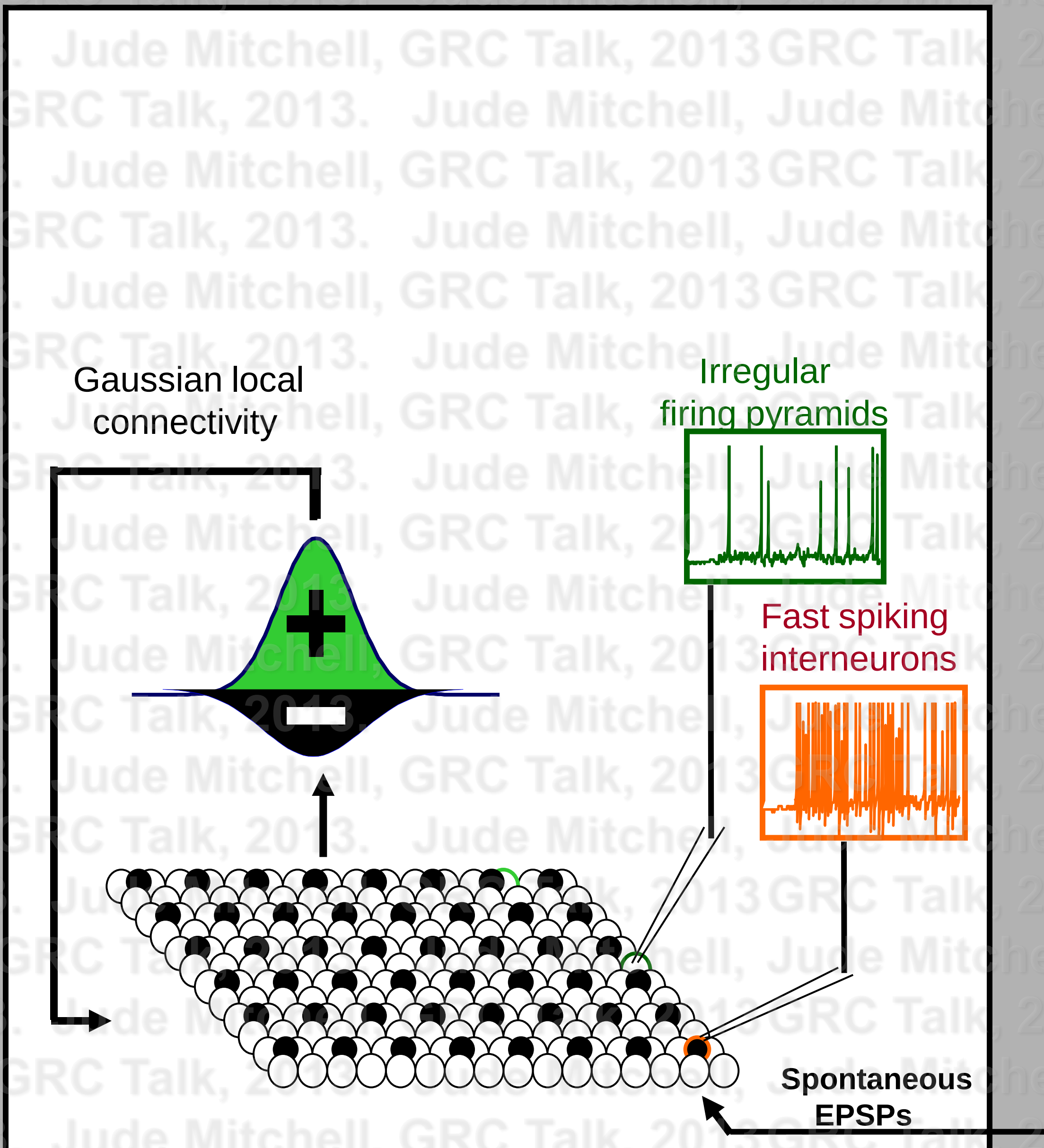
# Model architecture



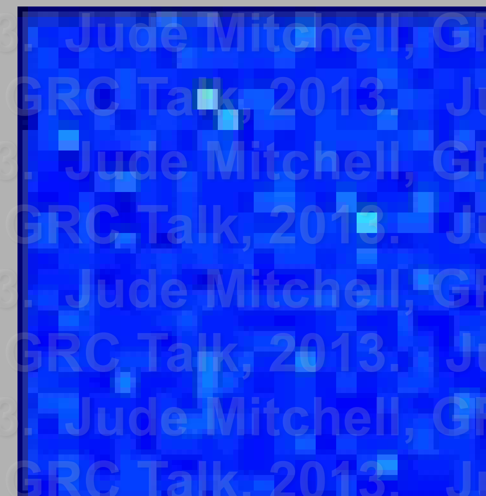

**Spontaneous Activity?**

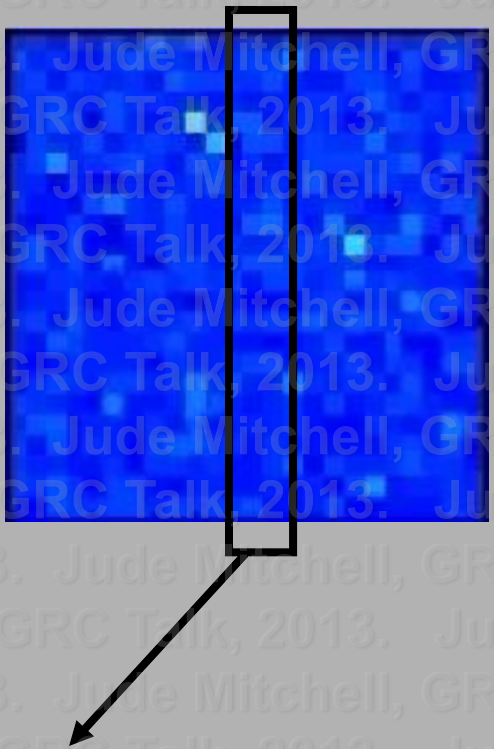


# Model architecture

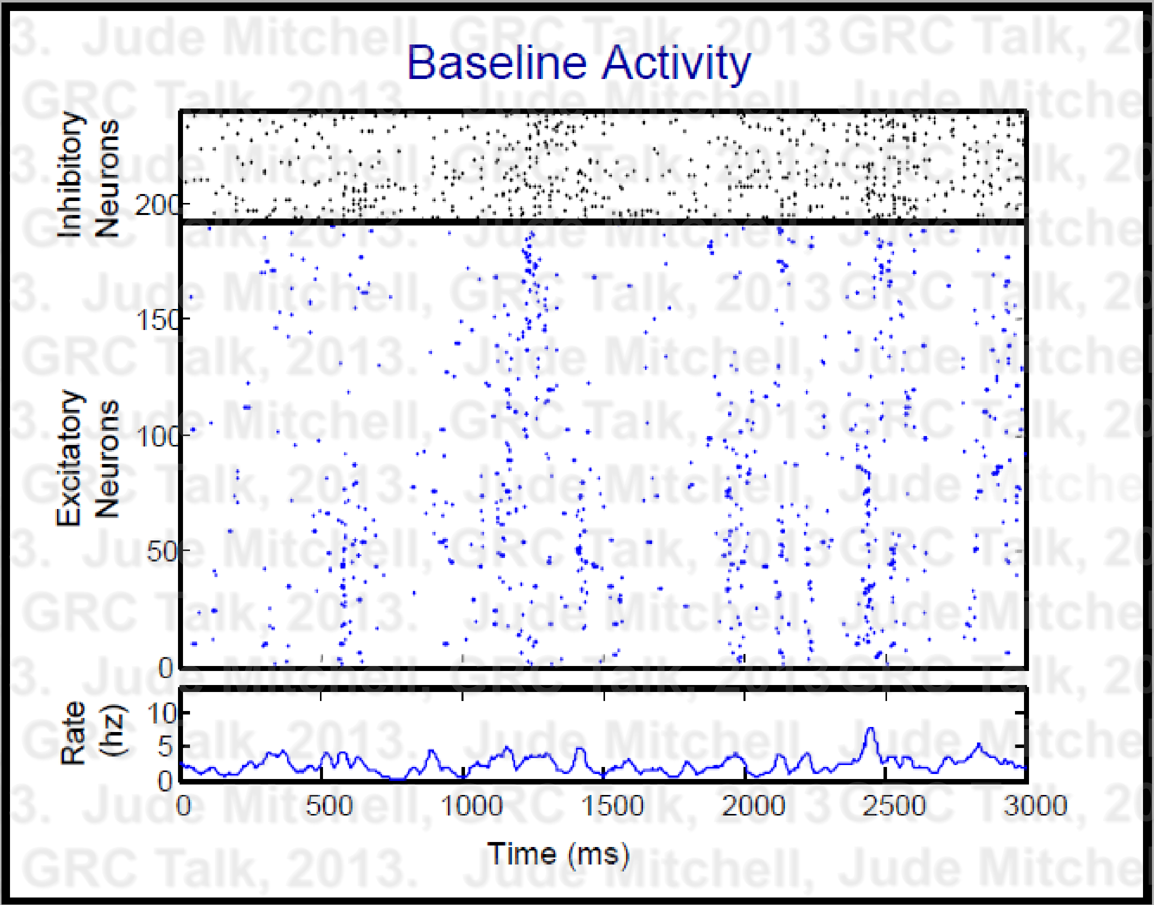


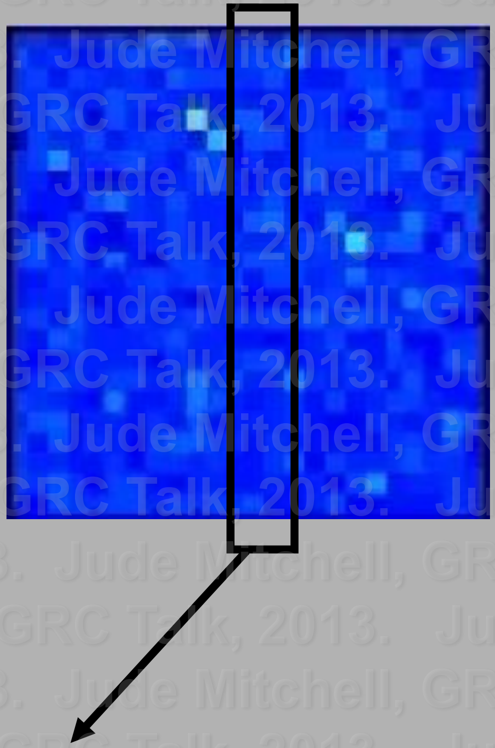

**Spontaneous Activity?**



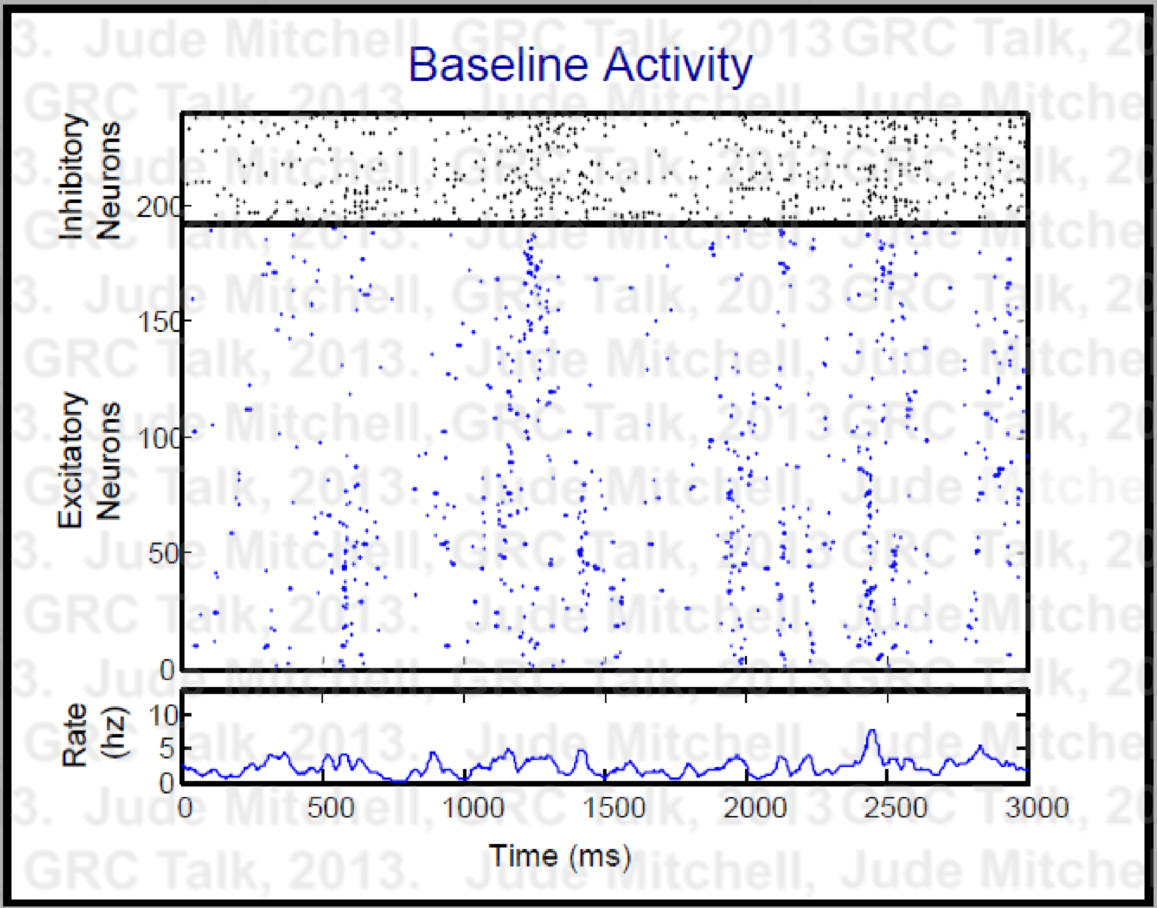


**Show activity as a raster of population spiking**

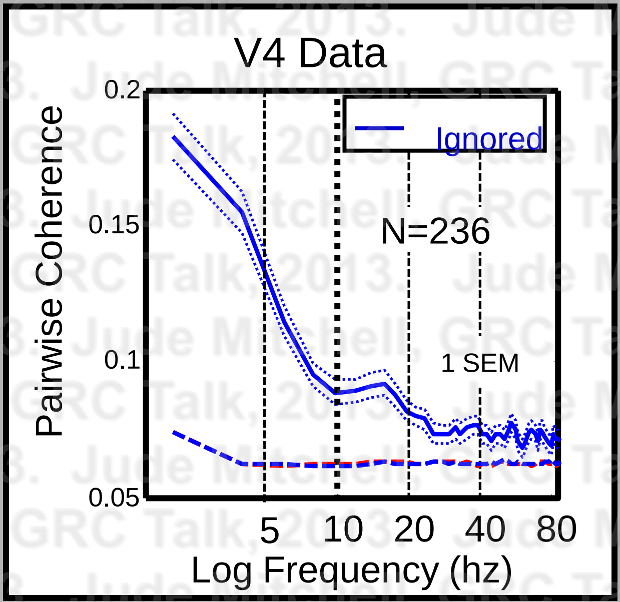


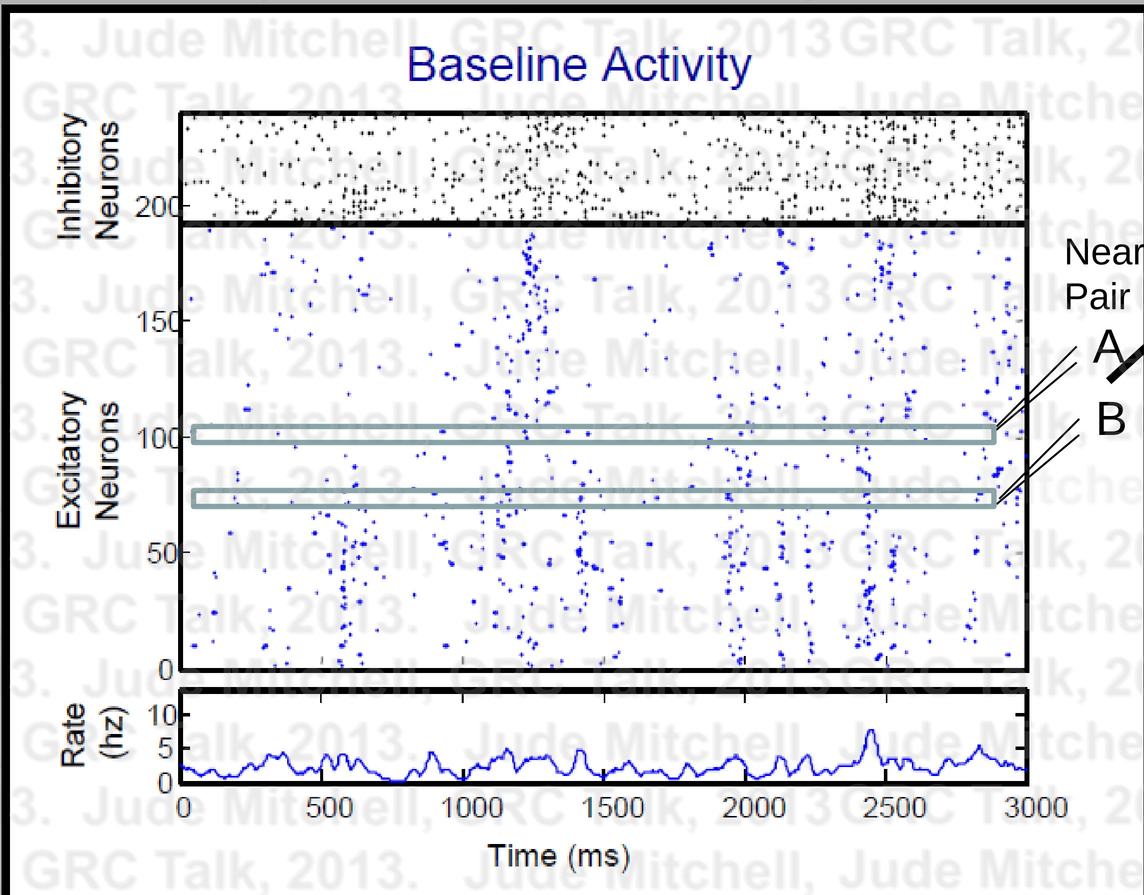



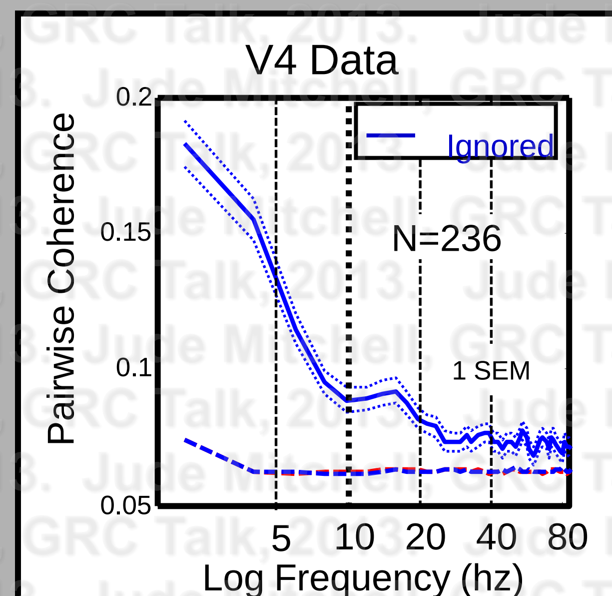
**Show activity as a raster of population spiking**

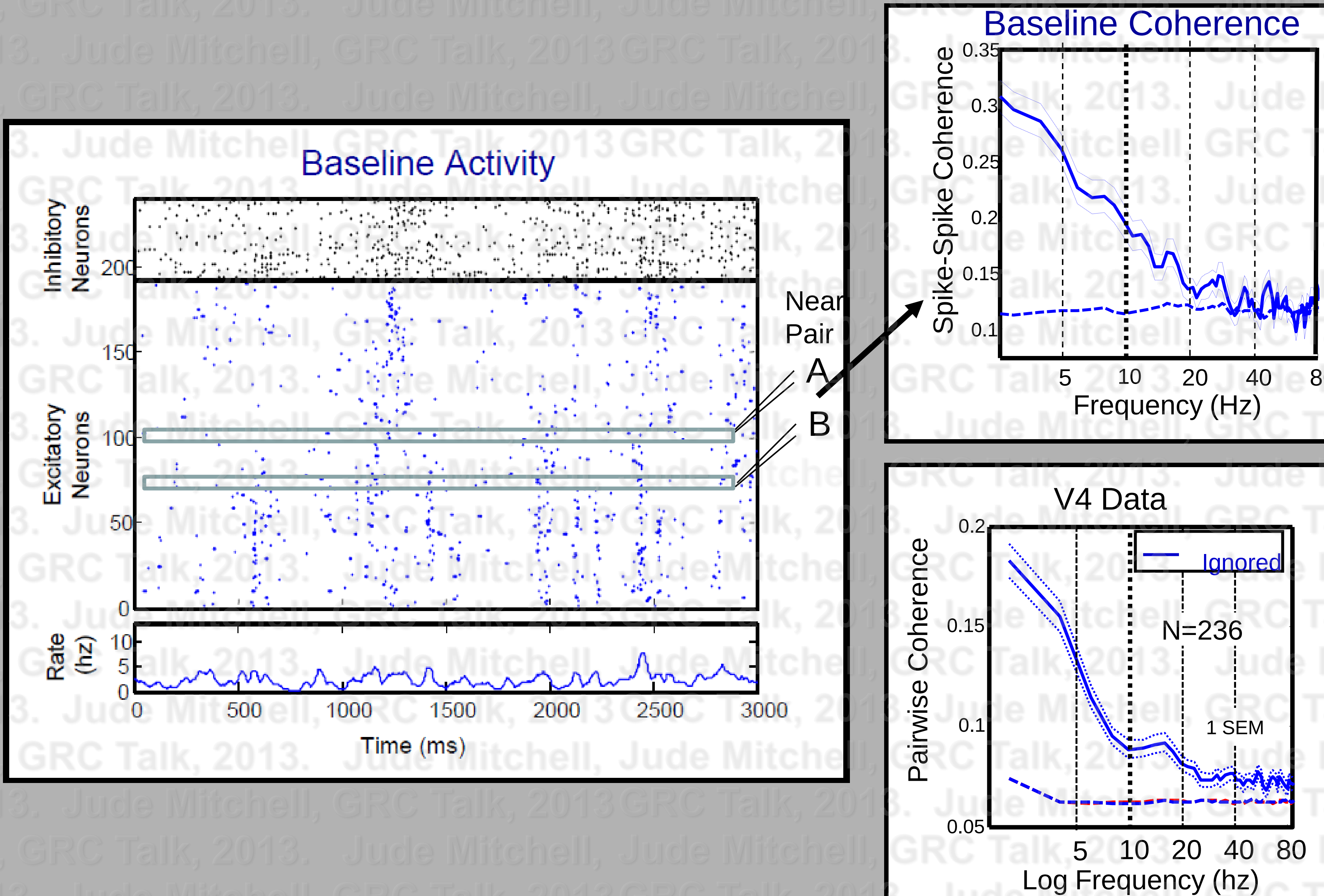



Do these fluctuations match that seen in the V4 data?



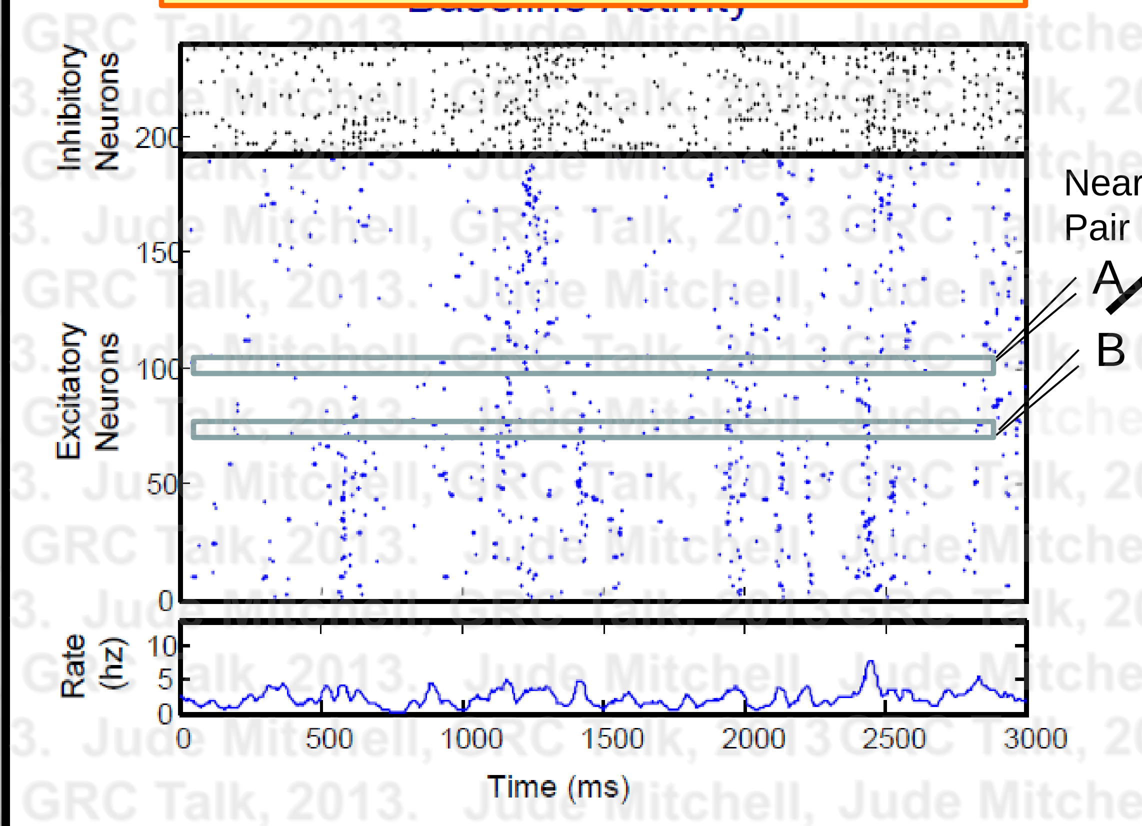

Baseline Activity
Inhibitory Neurons
Excitatory Neurons
200
150
100
50
0
Rate (hz)
10
5
0
0
500
1000
1500
2000
2500
3000
Time (ms)
Near Pair
A
B

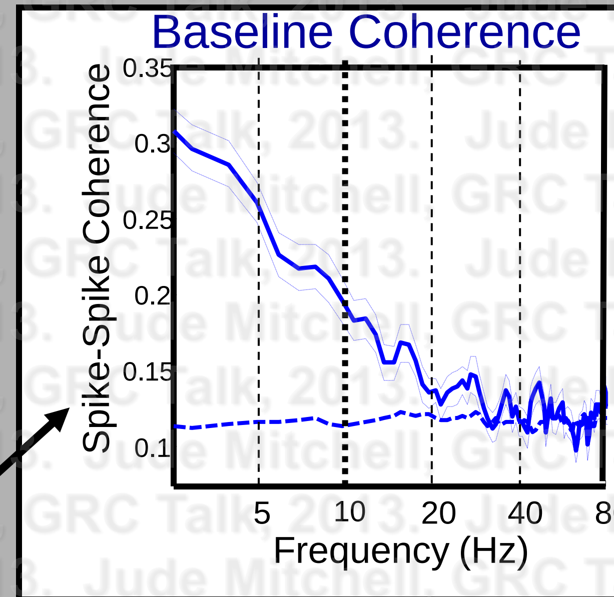

V4 Data
Pairwise Coherence
0.2
0.15
0.1
0.05
Ignored
N=236
1 SEM
5
10
20
40
80
Log Frequency (hz)

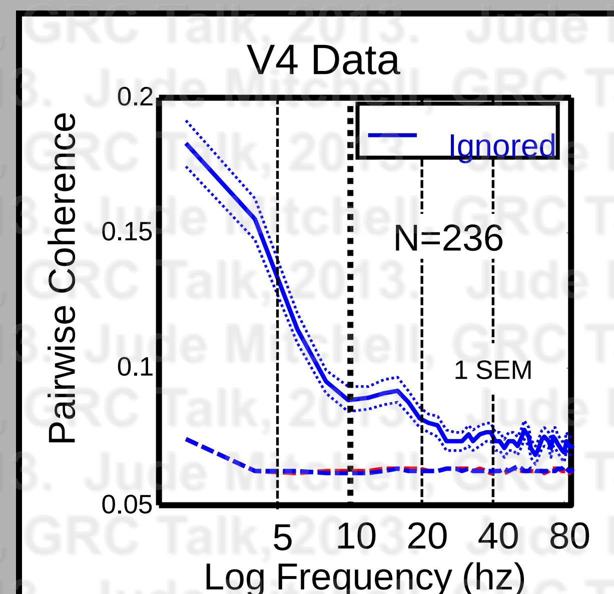

Baseline Activity
Inhibitory Neurons
Excitatory Neurons
Rate (hz)
Time (ms)
Near Pair
A
B
Baseline Coherence
Spike-Spike Coherence
Frequency (Hz)
V4 Data
Ignored
N=236
1 SEM
Pairwise Coherence
Log Frequency (hz)

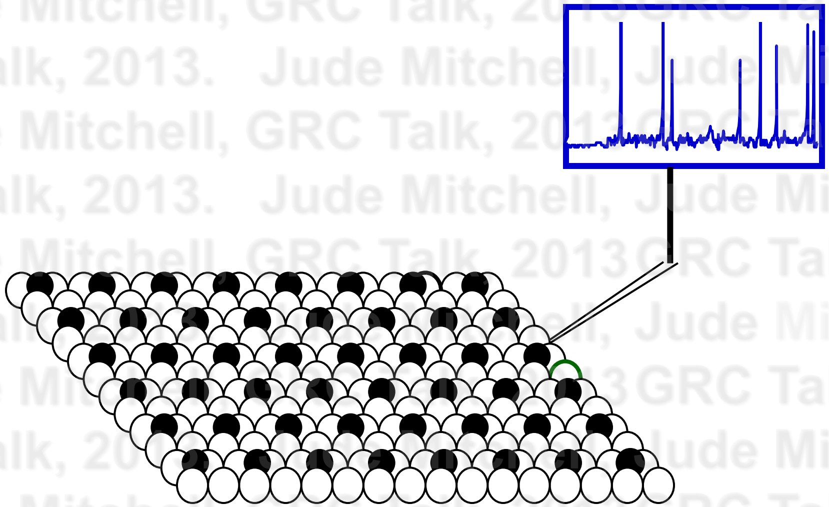
What model parameters are essential to the shared fluctuations?

- spiking neurons
- strong recurrent connections
- balanced excitation/inhibition
- slower NMDA currents



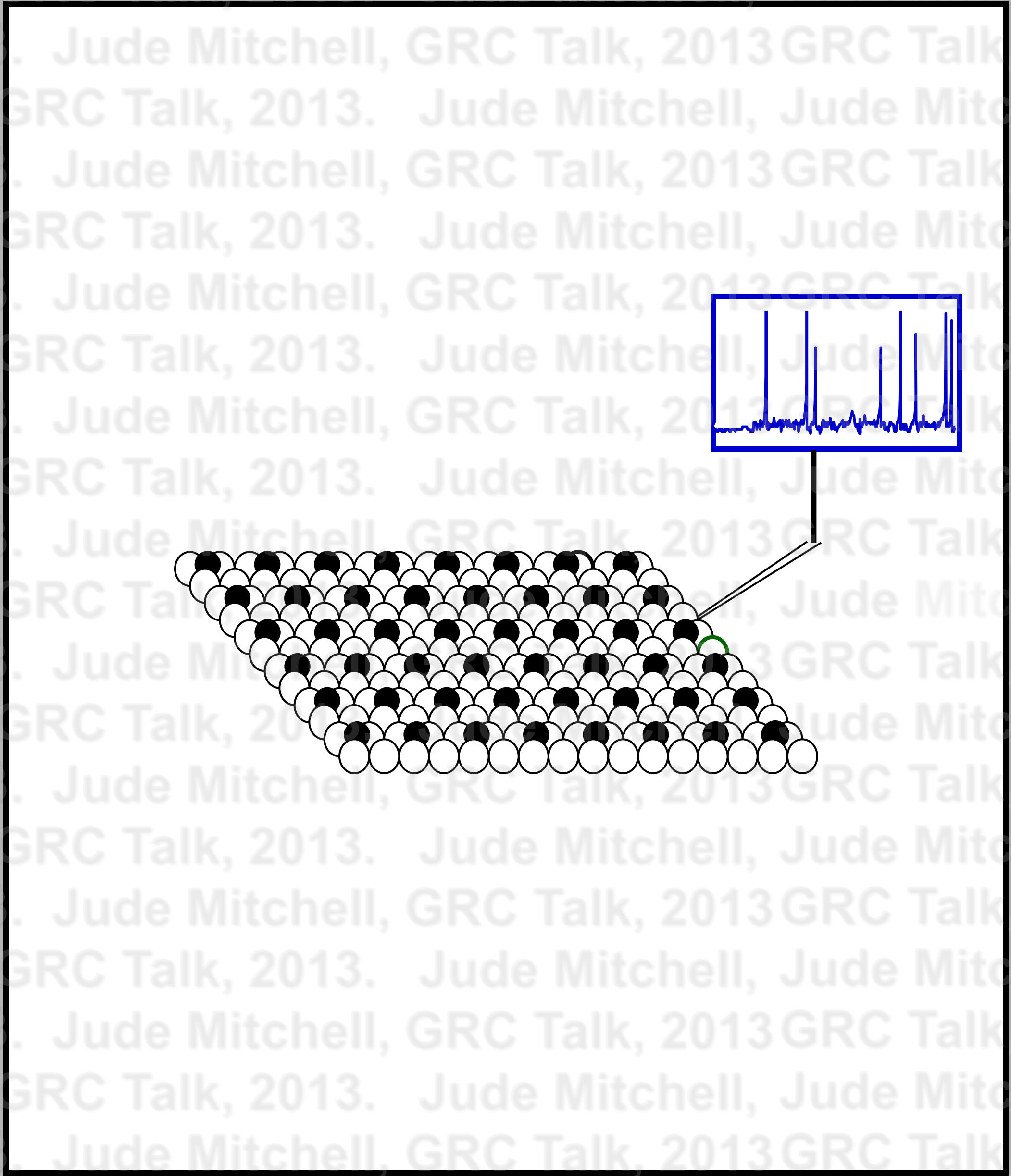





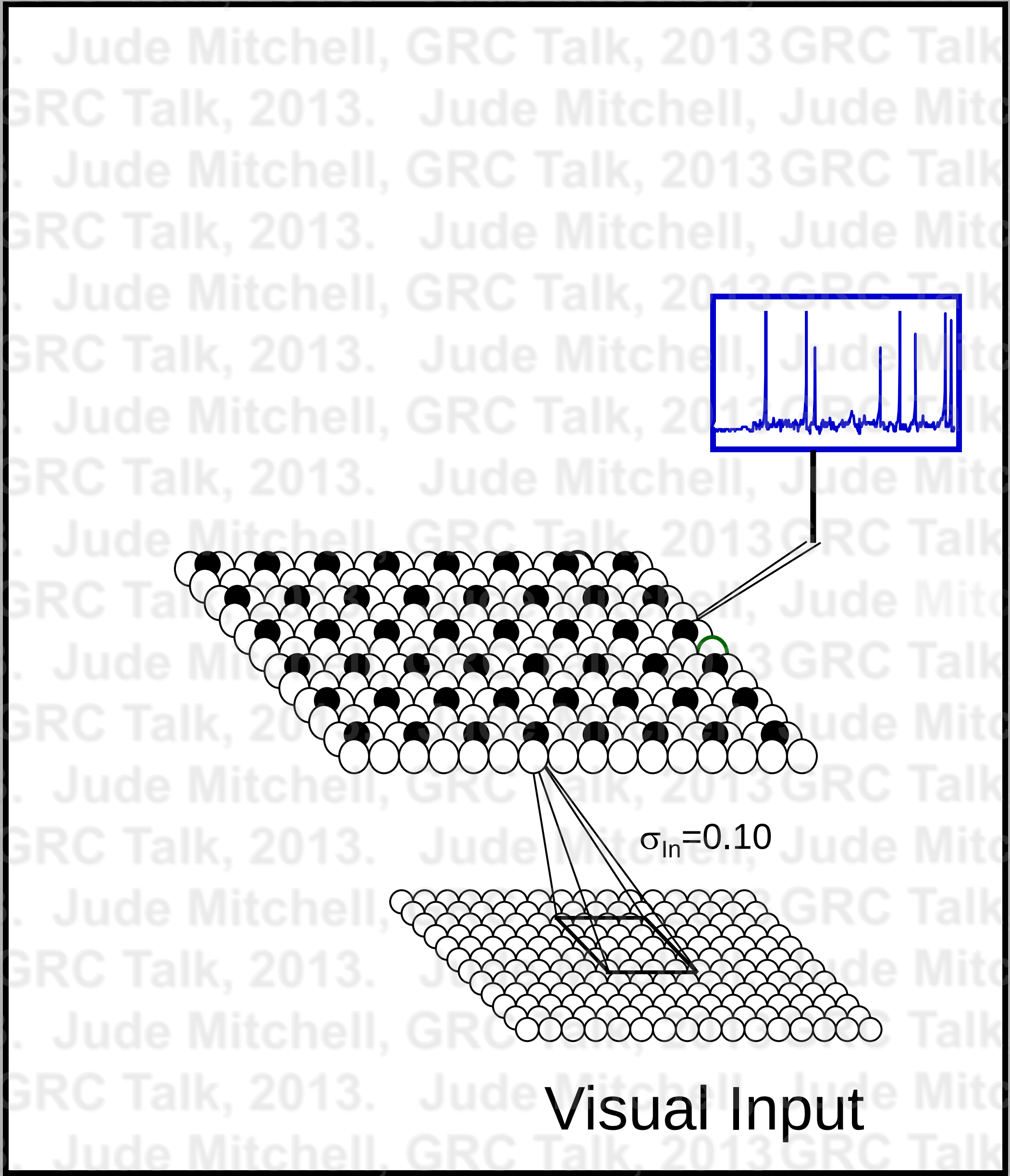
# Sensory input reduces ongoing activity

(Smith & Kohn, 2008;
Churchland et al, 2009)



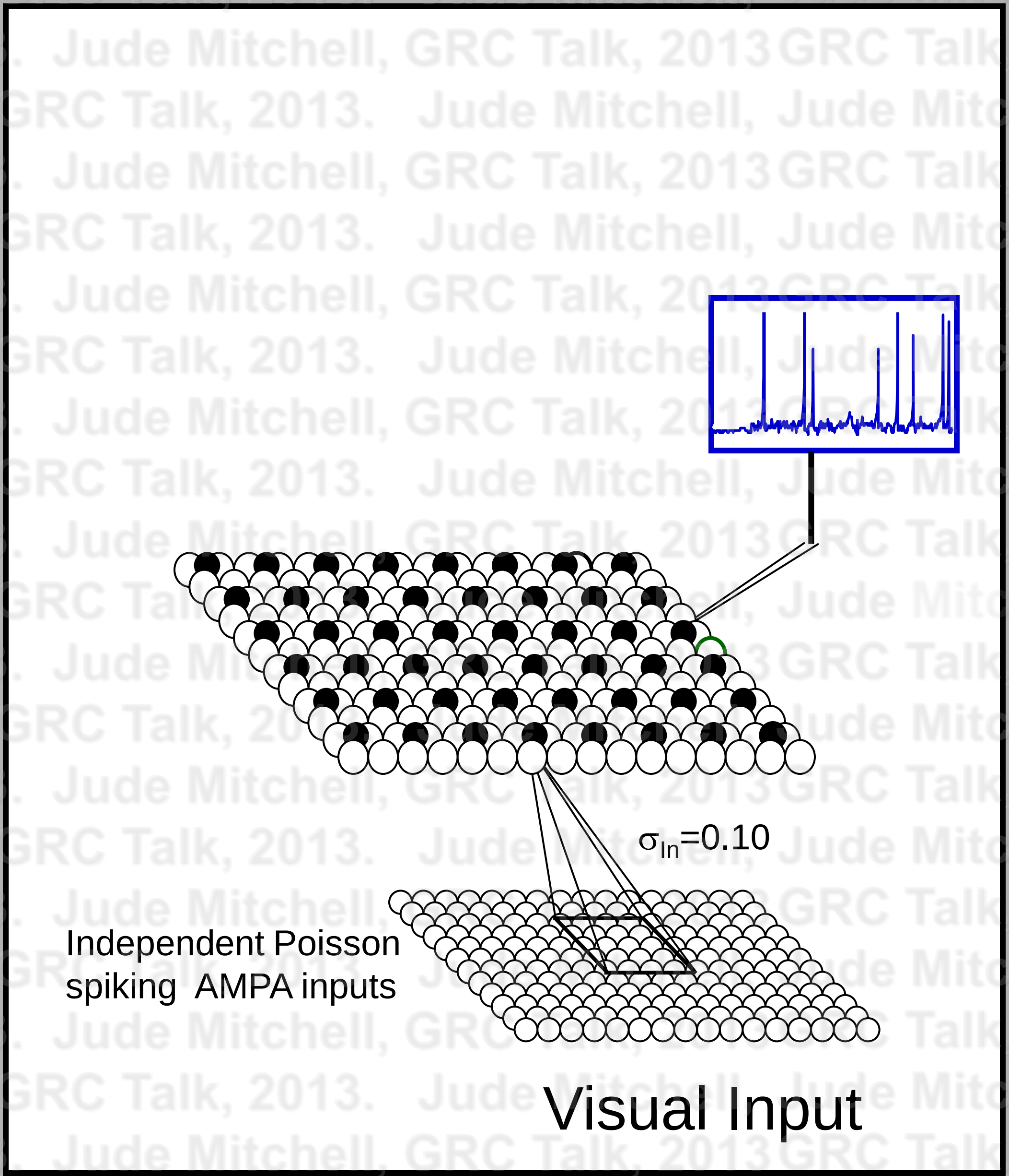
# Sensory input reduces ongoing activity

(Smith & Kohn, 2008;
Churchland et al, 2009)



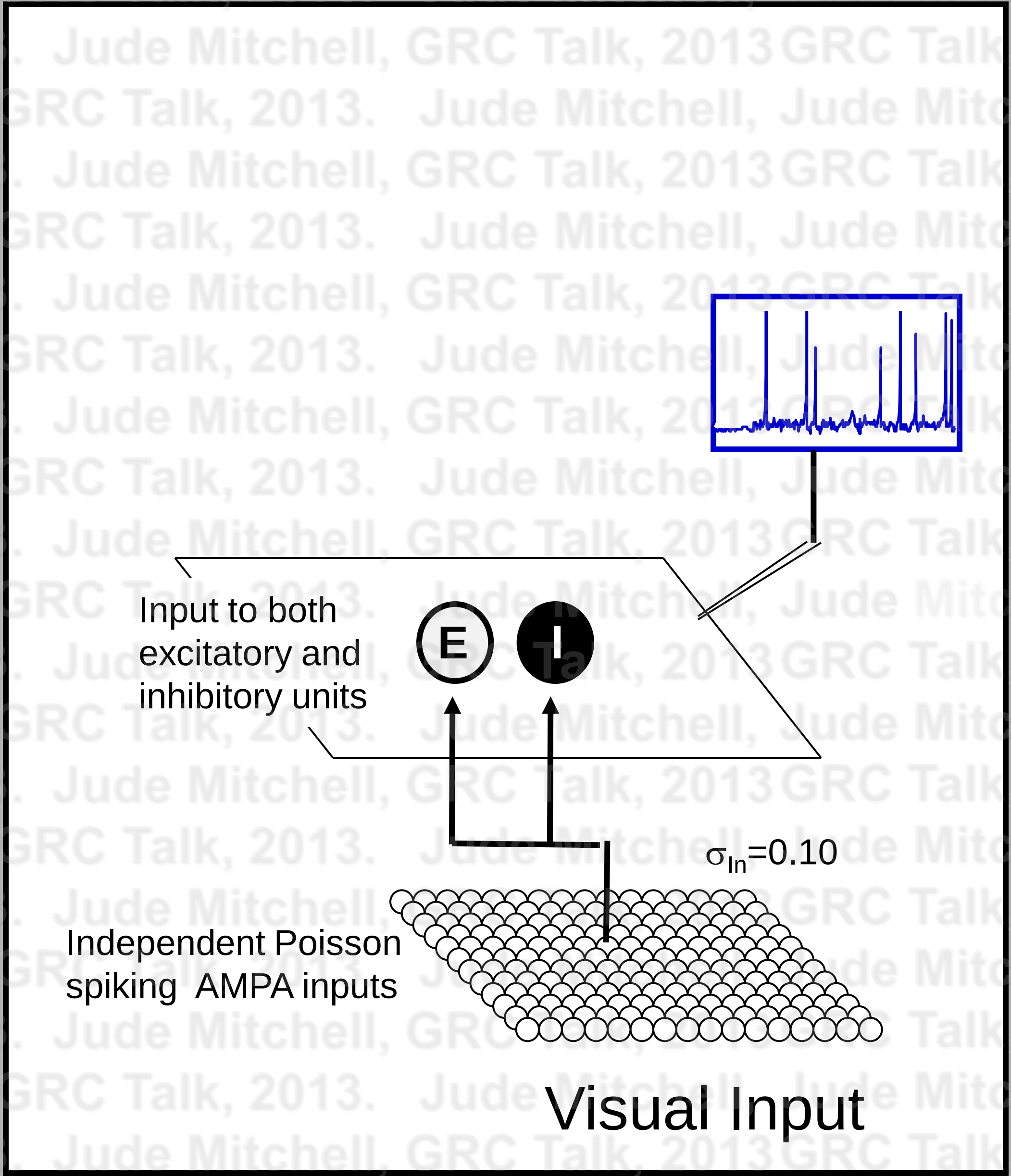
# Sensory input reduces ongoing activity

(Smith & Kohn, 2008; Churchland et al, 2009)



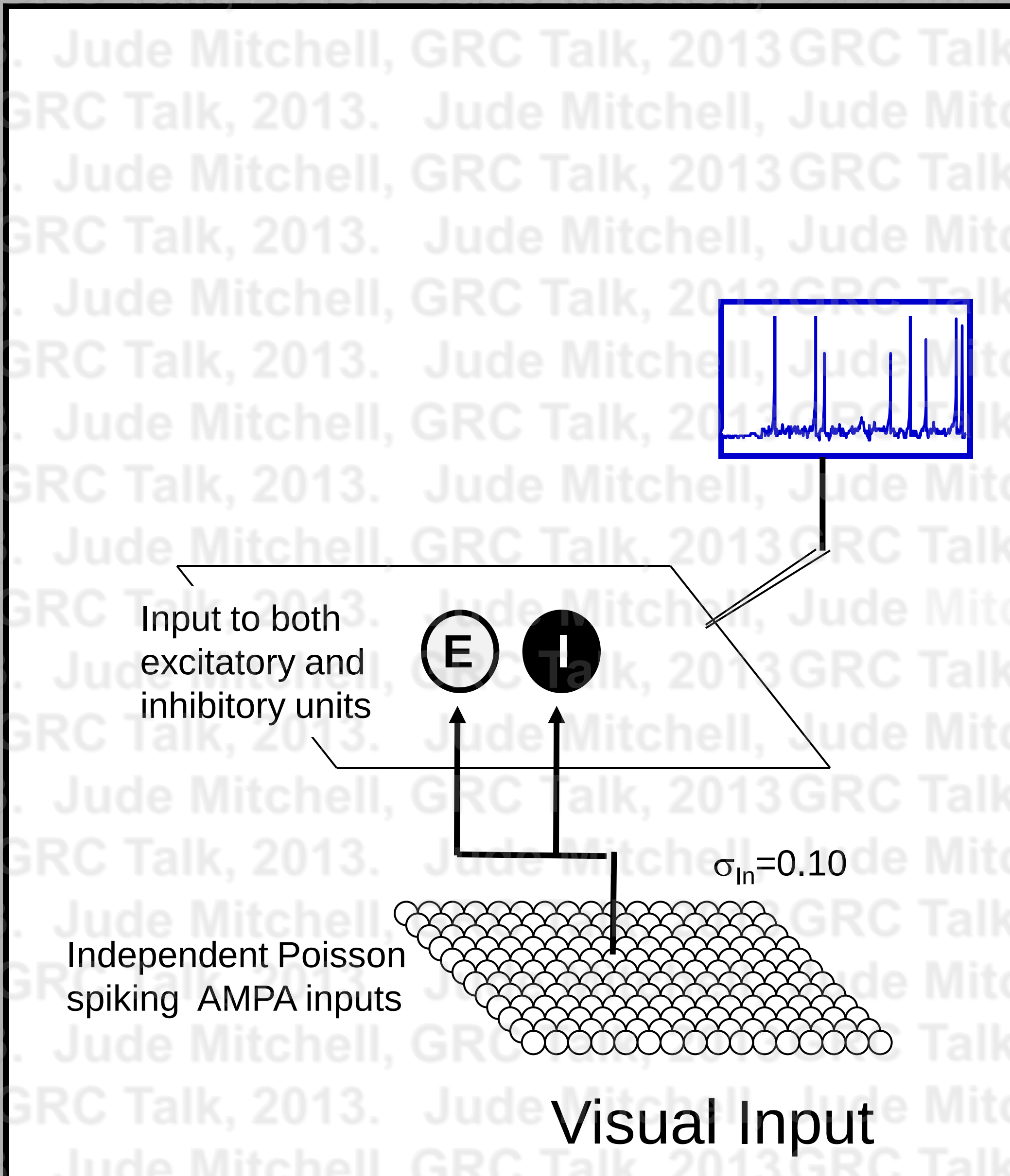
# Sensory input reduces ongoing activity

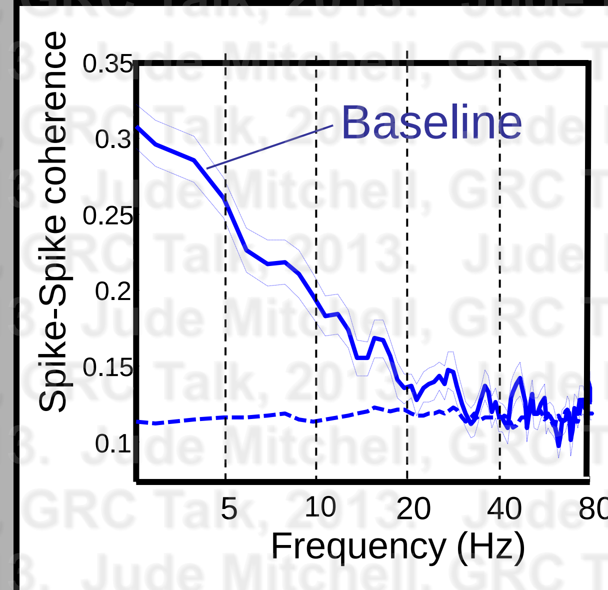
(Smith & Kohn, 2008; Churchland et al, 2009)

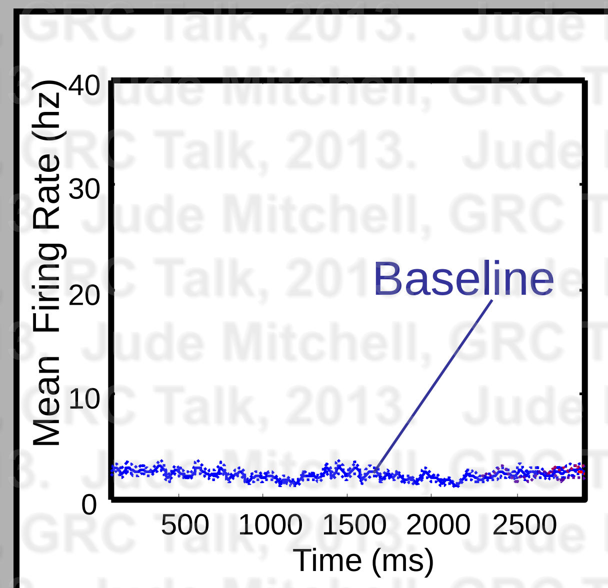


# Sensory input reduces ongoing activity

(Smith & Kohn, 2008; Churchland et al, 2009)

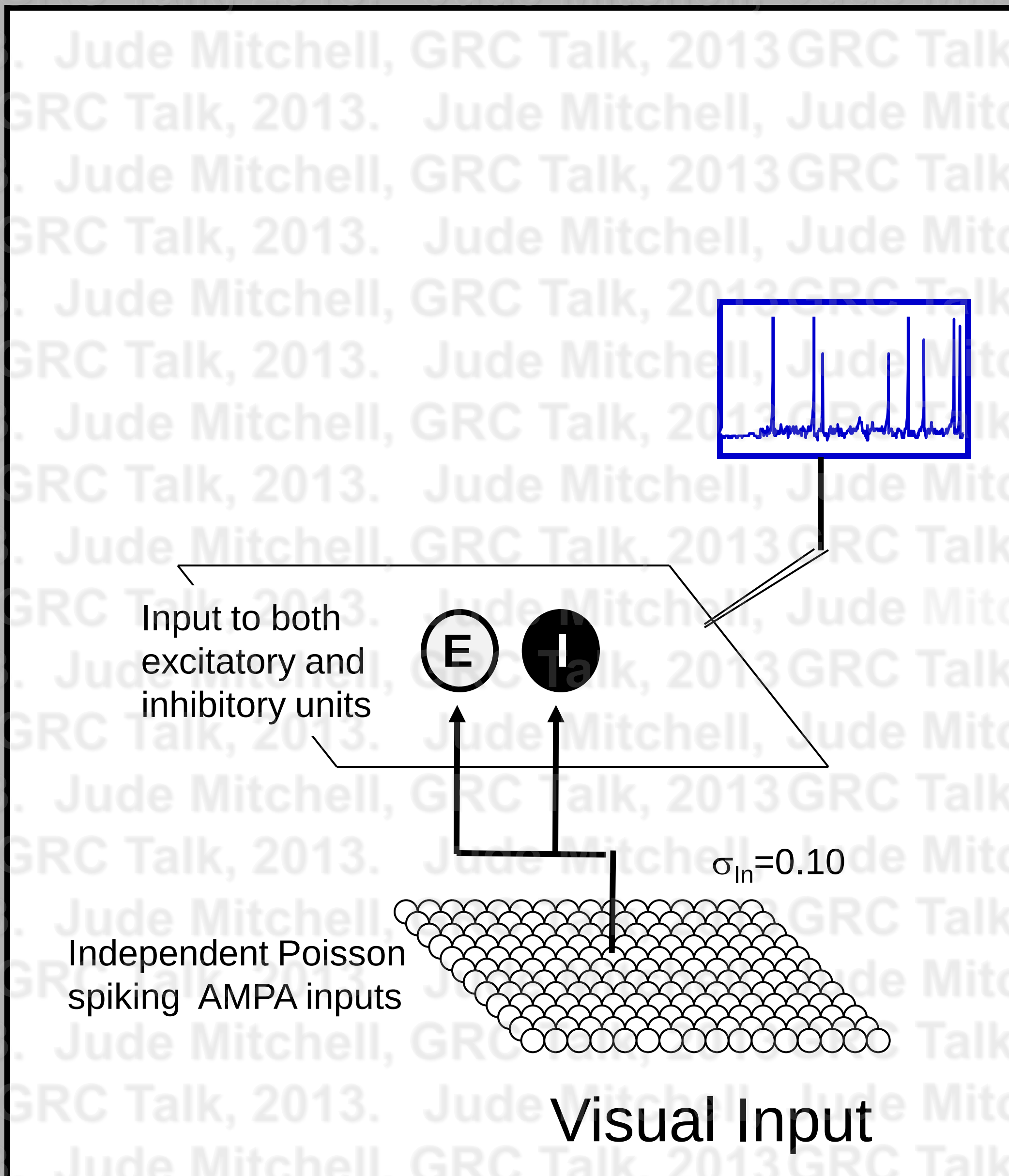


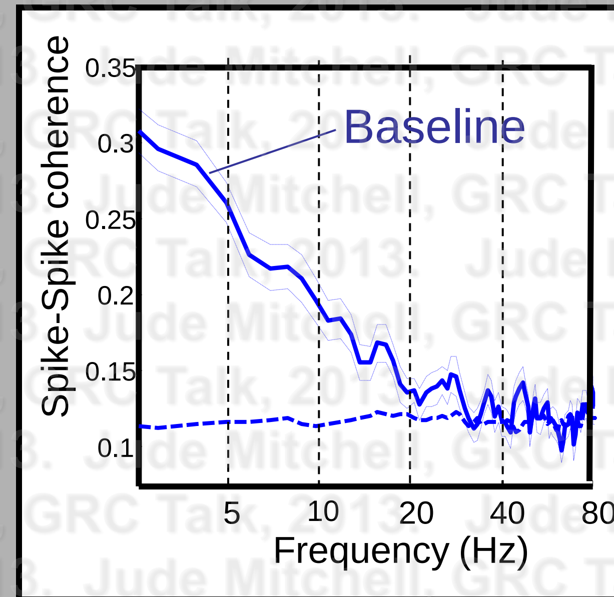



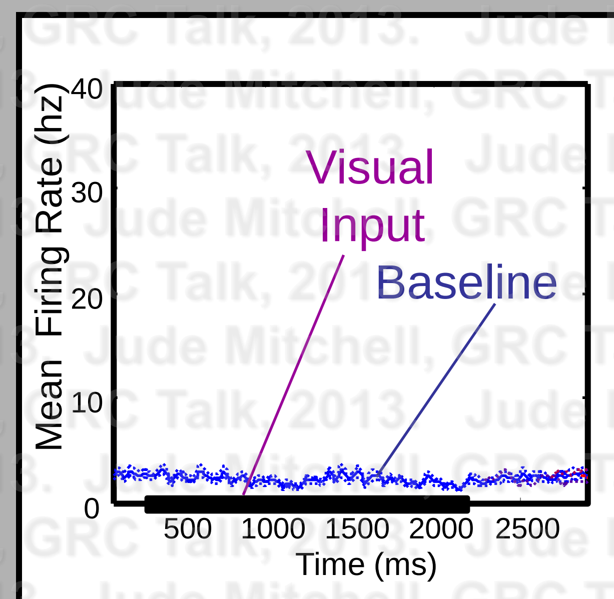



# Sensory input reduces ongoing activity

(Smith & Kohn, 2008; Churchland et al, 2009)

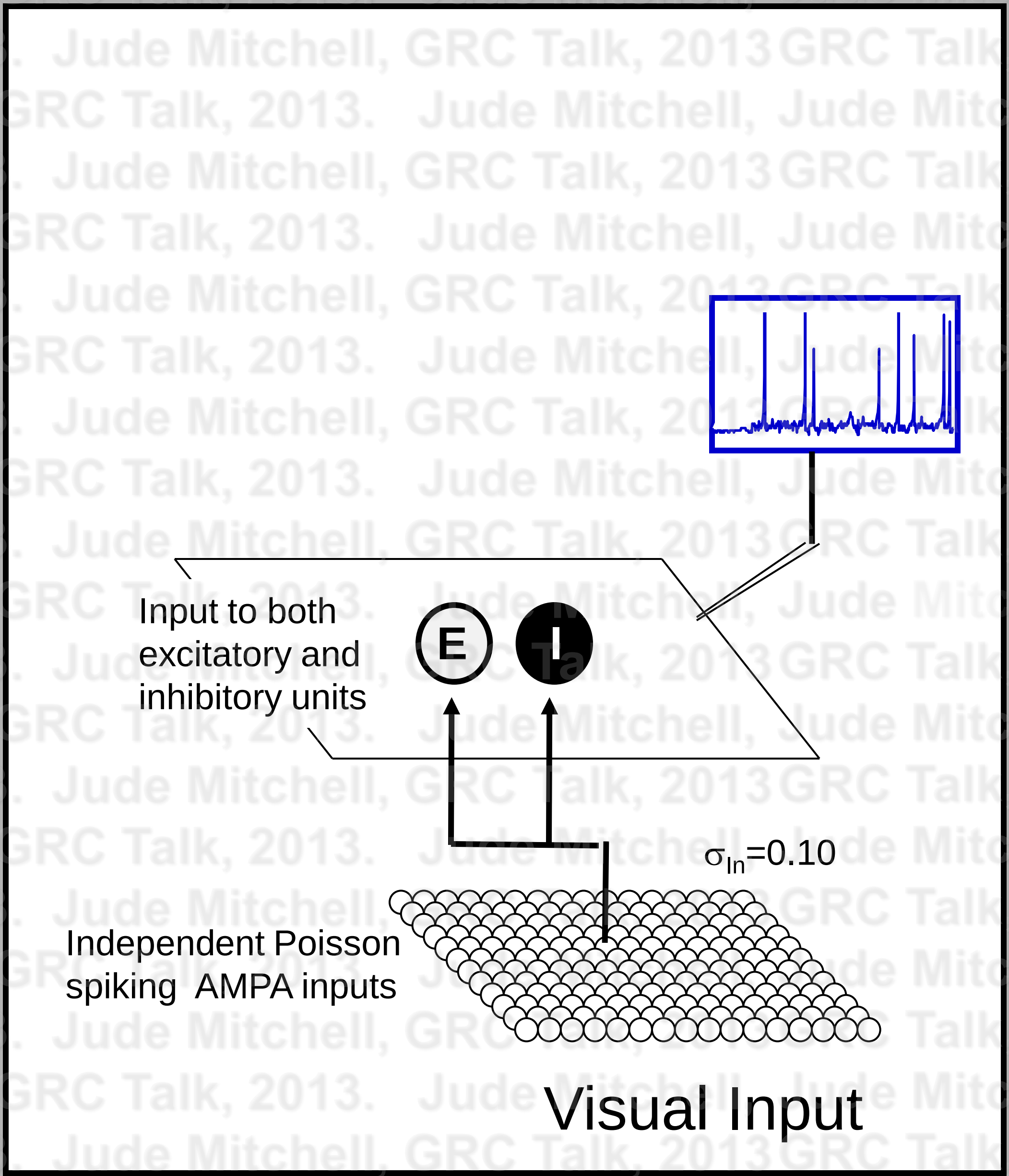


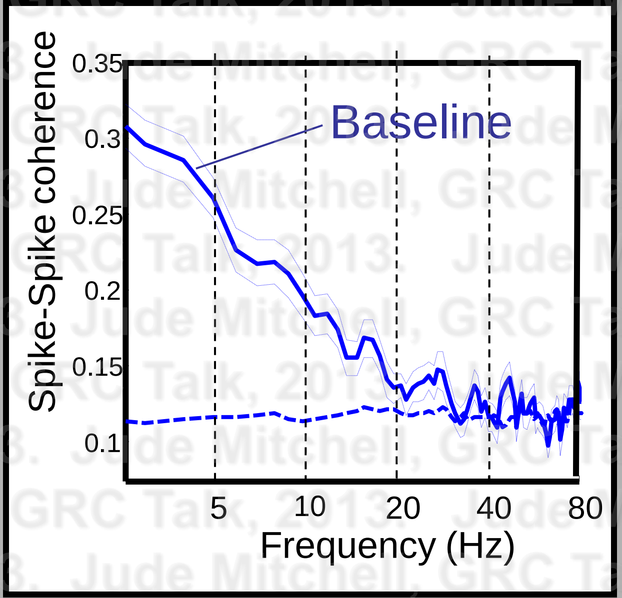



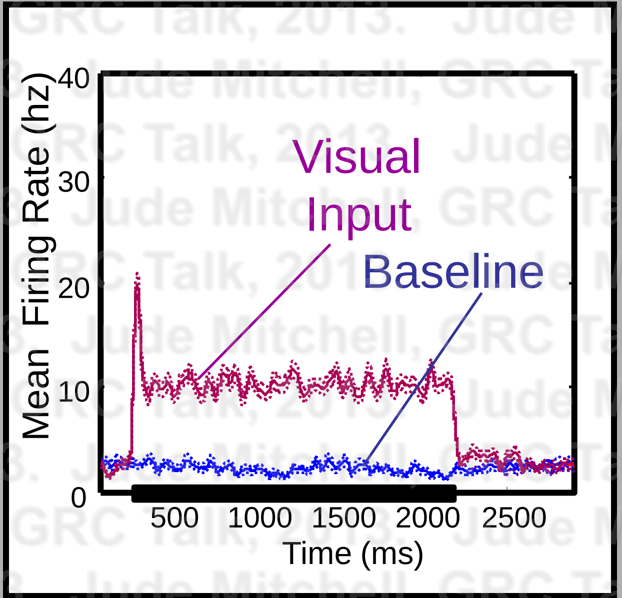



# Sensory input reduces ongoing activity

(Smith & Kohn, 2008; Churchland et al, 2009)



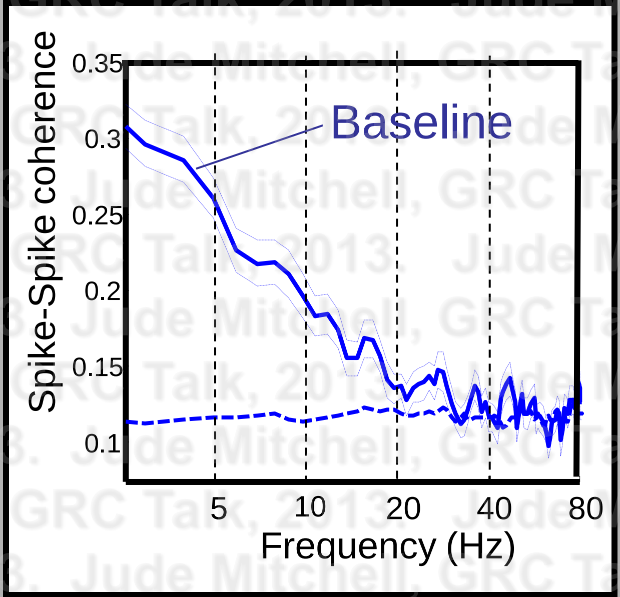



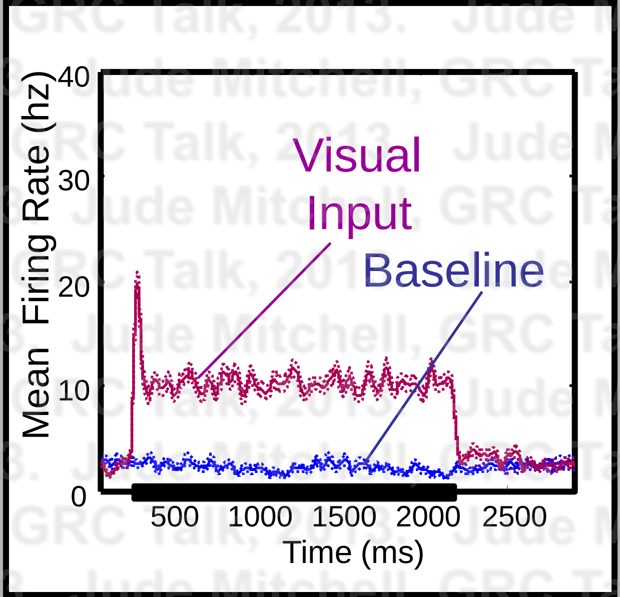



# Sensory input reduces ongoing activity

(Smith & Kohn, 2008;
Churchland et al, 2009)

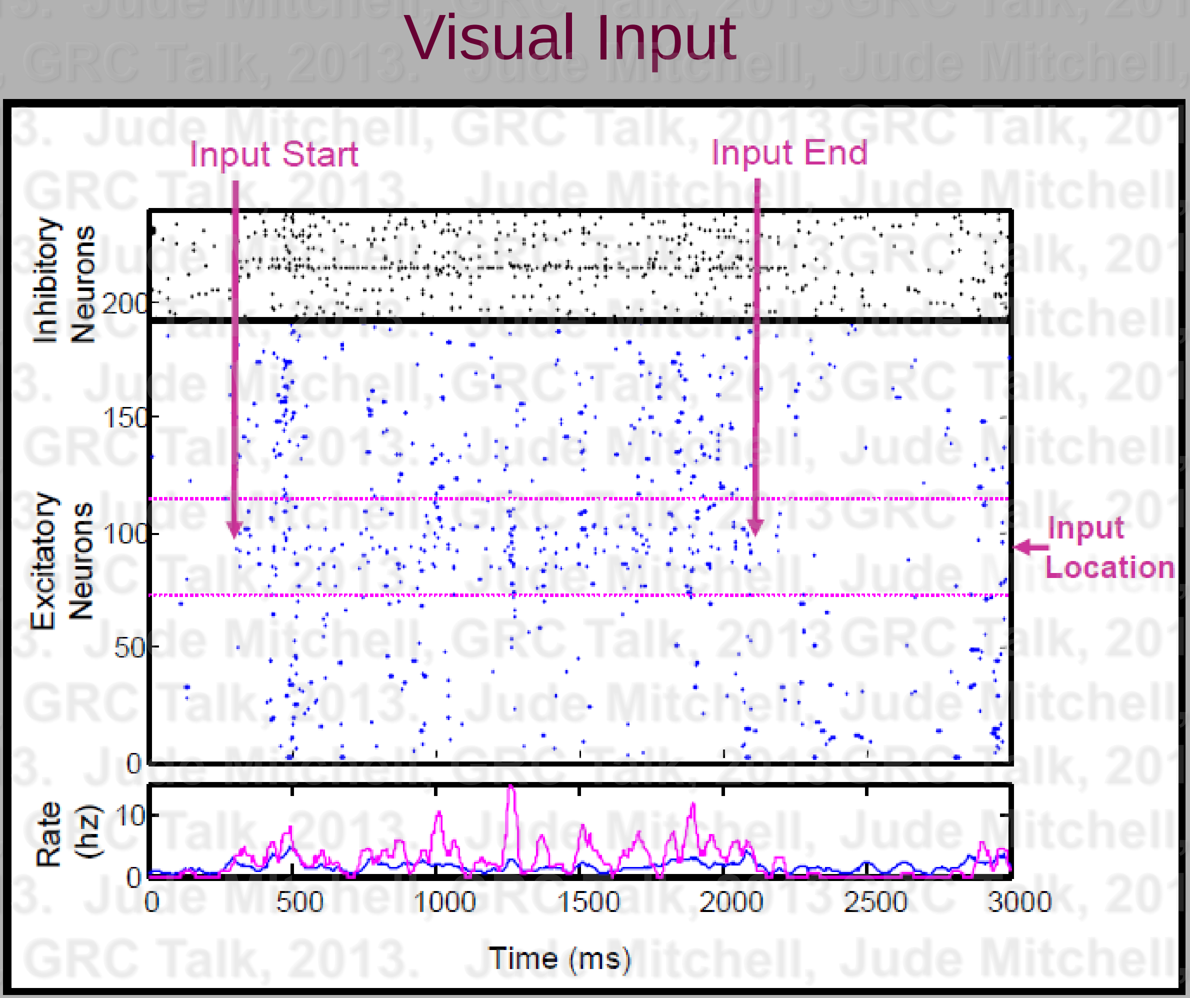
Visual Input

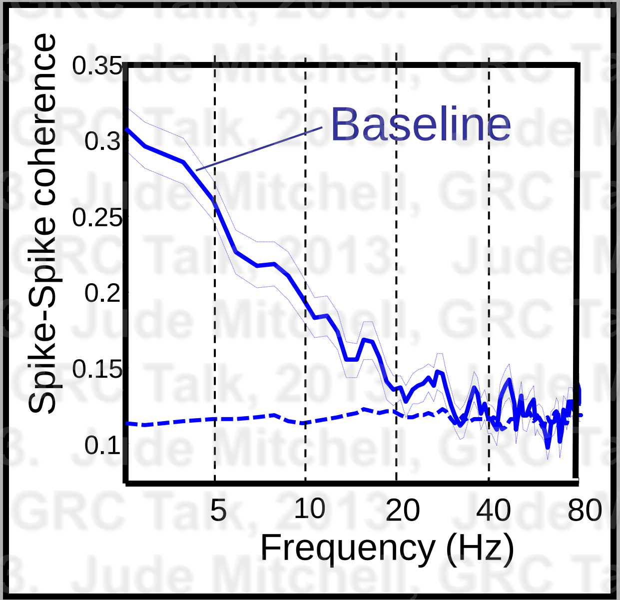


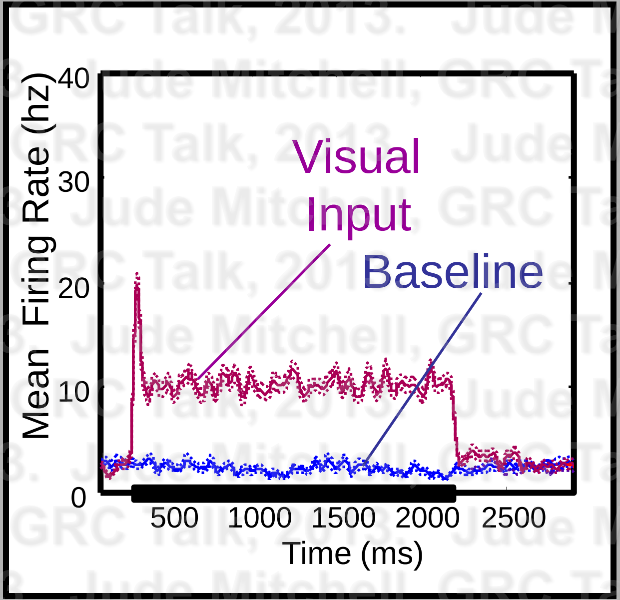



# Sensory input reduces ongoing activity

(Smith & Kohn, 2008; Churchland et al, 2009)



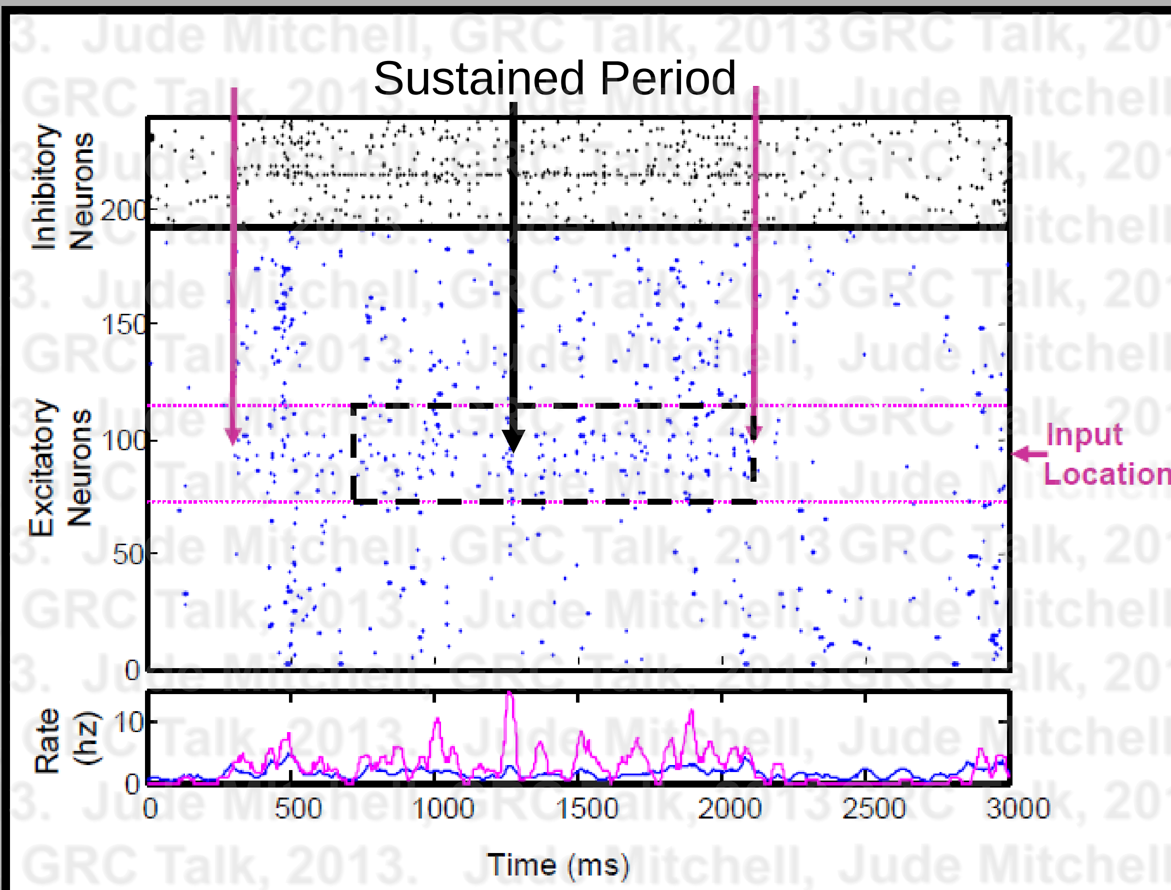



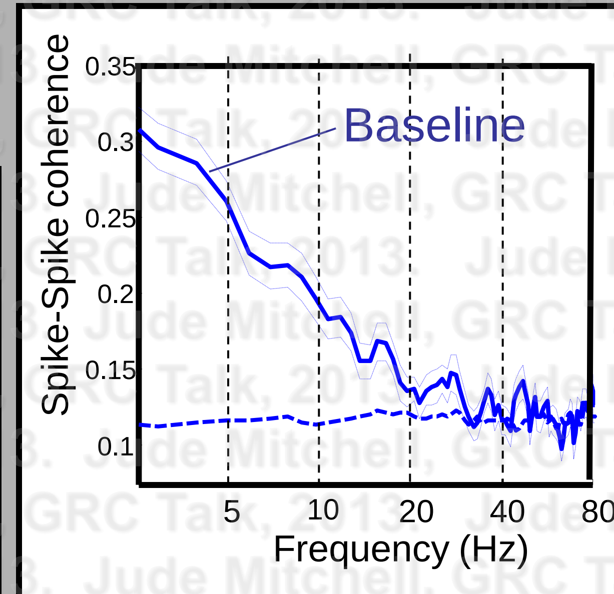



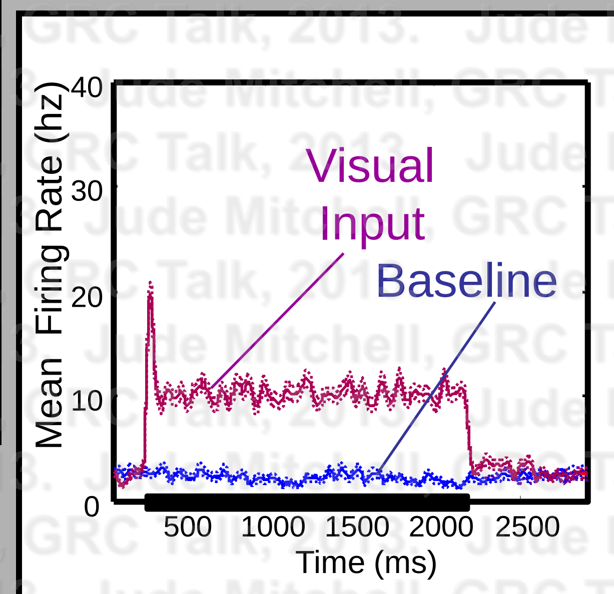
# Sensory input reduces ongoing activity

(Smith & Kohn, 2008; Churchland et al, 2009)

## Visual Input



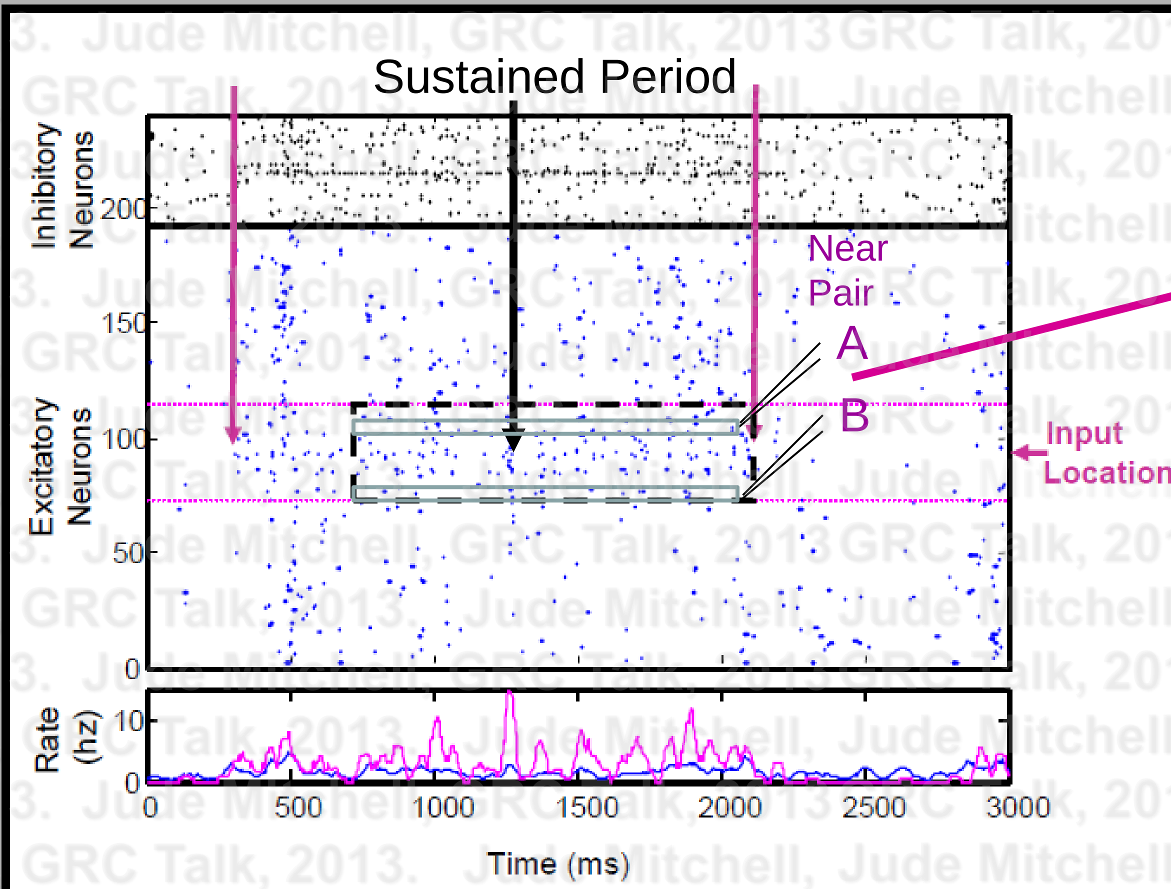



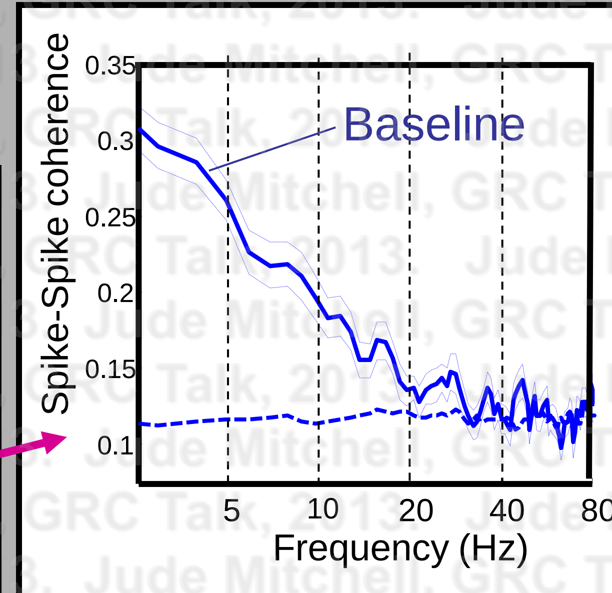



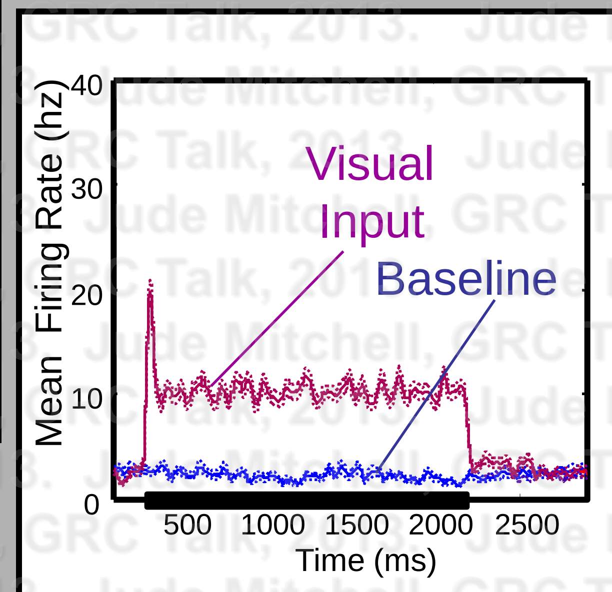
# Sensory input reduces ongoing activity

(Smith & Kohn, 2008; Churchland et al, 2009)

Visual Input

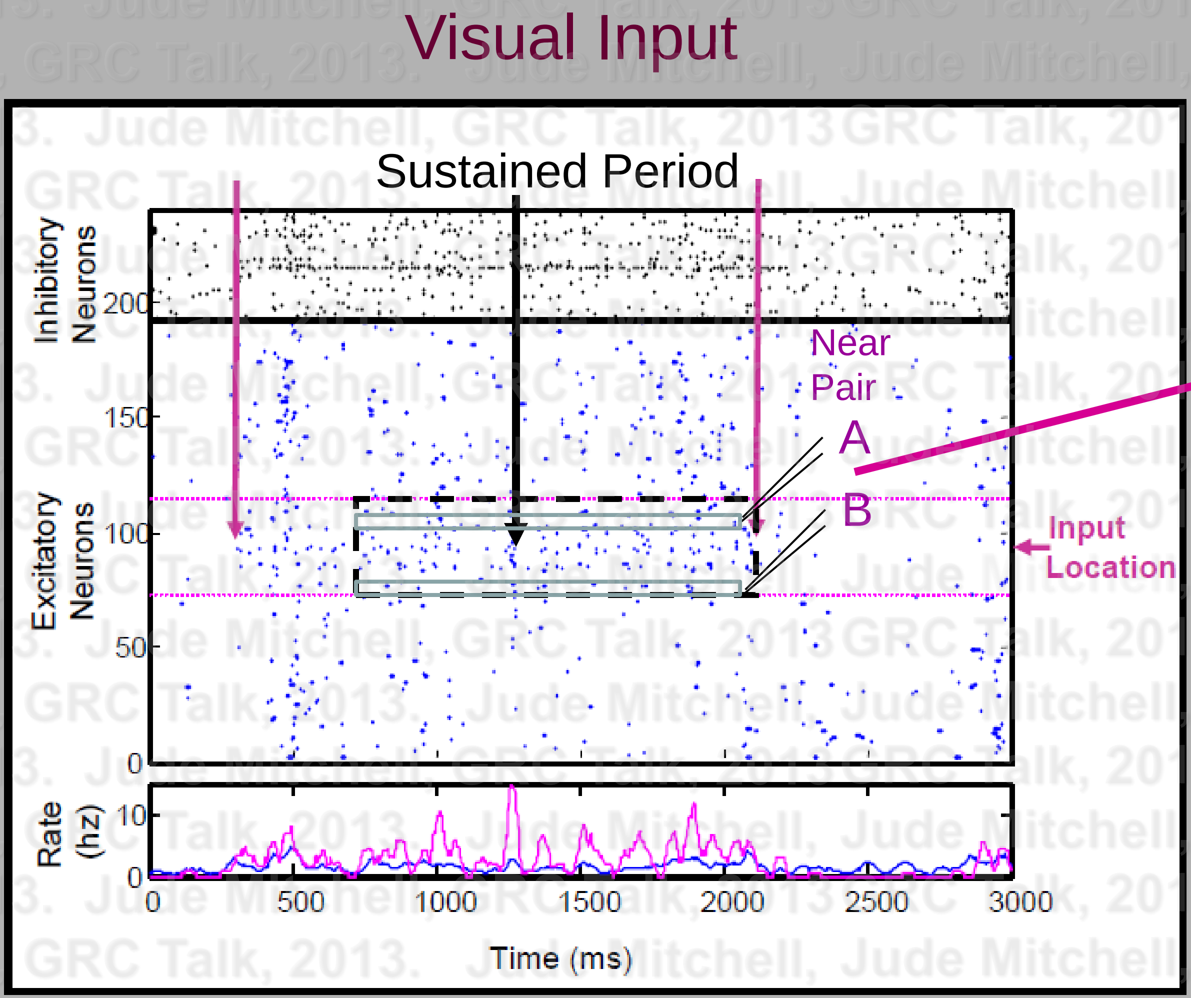


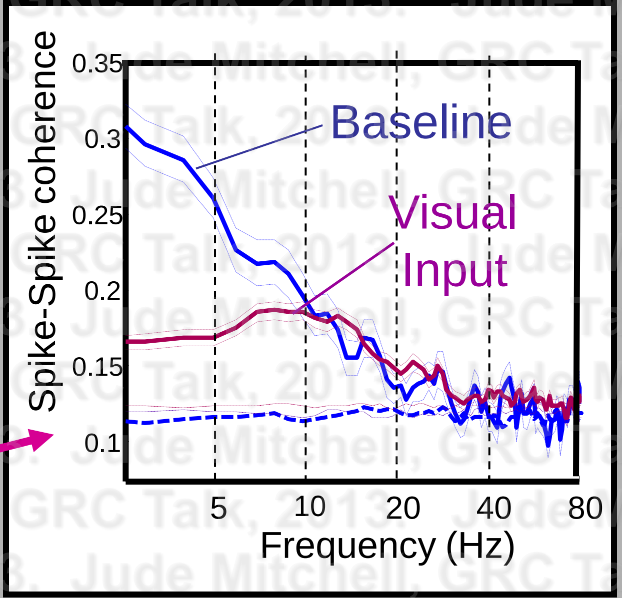



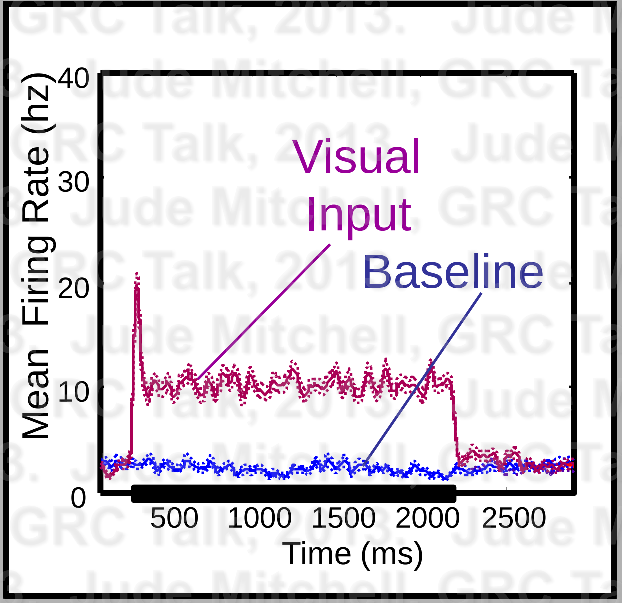



# Sensory input reduces ongoing activity

(Smith & Kohn, 2008; Churchland et al, 2009)



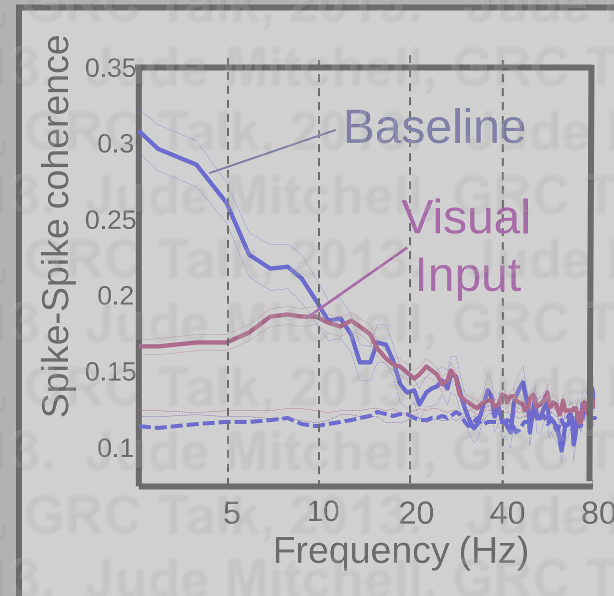



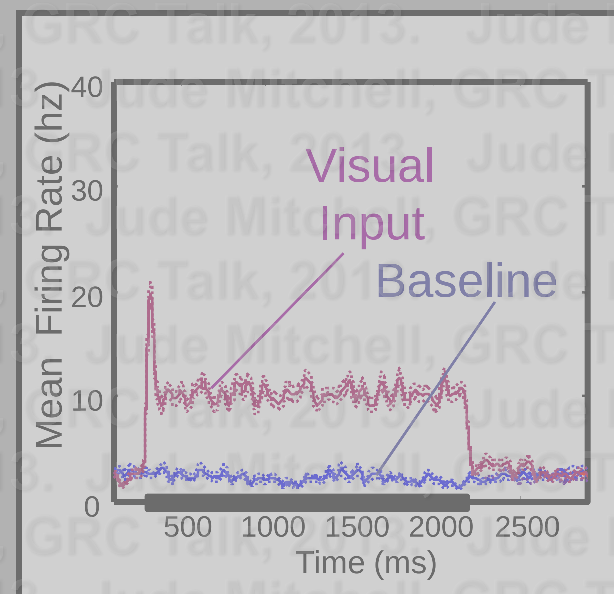



# Sensory input reduces ongoing activity

(Smith & Kohn, 2008; Churchland et al, 2009)

## Why does visual input reduce ongoing activity?



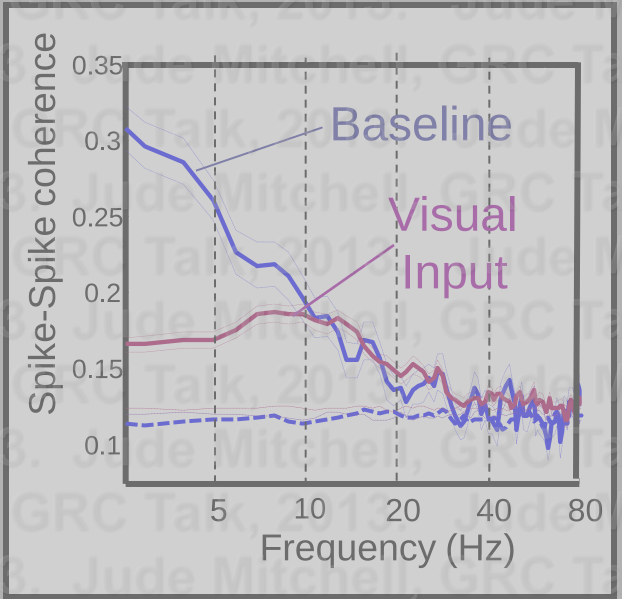
# Sensory input reduces ongoing activity

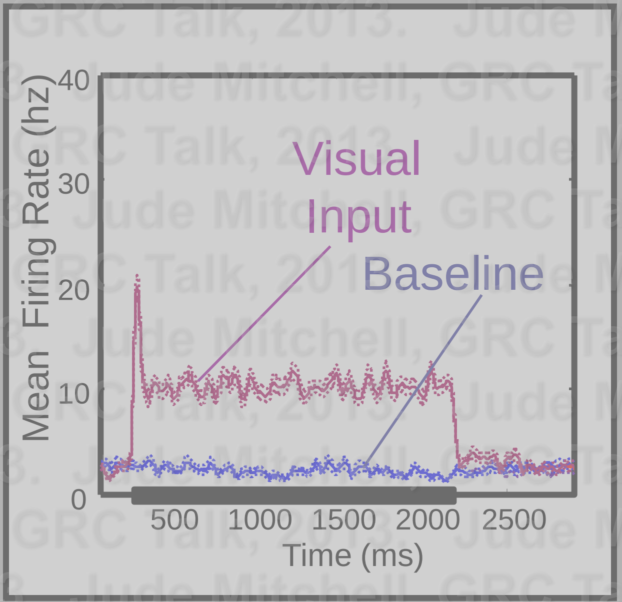
(Smith & Kohn, 2008; Churchland et al, 2009)

## Why does visual input reduce ongoing activity?

$$\tau \, dV/dt = g_{FF}(E_{FF} - V) + g_{REC}(E_{REC} - V)$$

(Integrate and fire neurons)



# Sensory input reduces ongoing activity

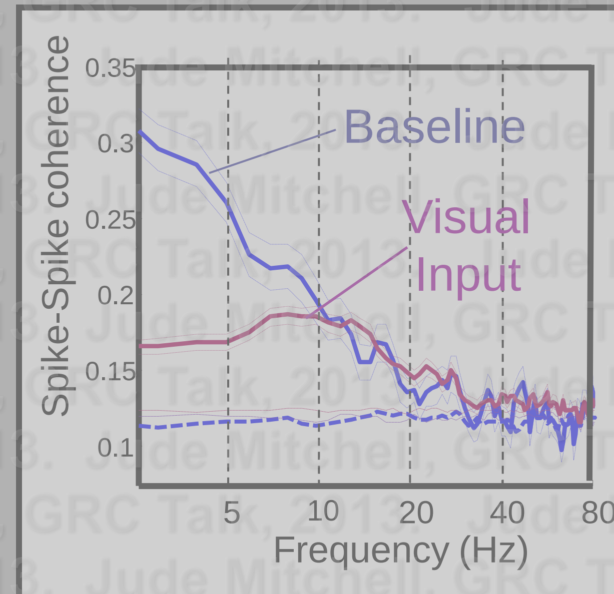
(Smith & Kohn, 2008; Churchland et al, 2009)

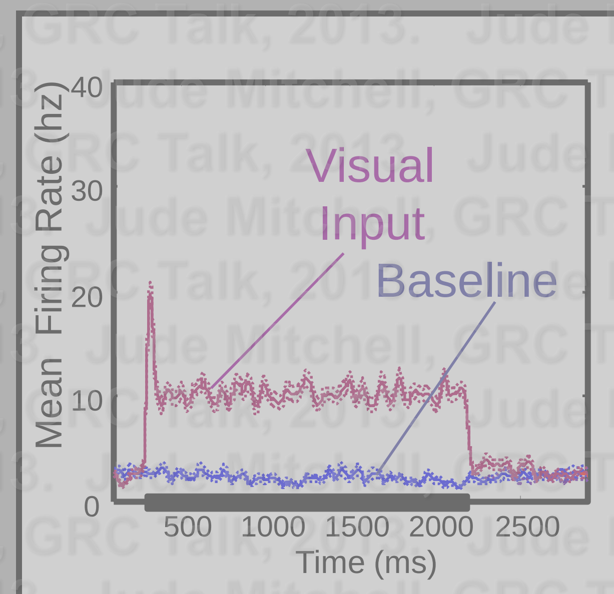
## Why does visual input reduce ongoing activity?

$$\tau \; dV/dt = g_{FF}\,(E_{FF} - V) + g_{REC}\,(E_{REC} - V)$$

$$V_{\infty} \cong \frac{g_{FF}\,E_{FF} + g_{REC}\,E_{REC}}{g_{FF} + g_{REC}}$$

Normalization = Weighted Averaging
Feed-forward vs Recurrent Terms



# Sensory input reduces ongoing activity

(Smith & Kohn, 2008; Churchland et al, 2009)

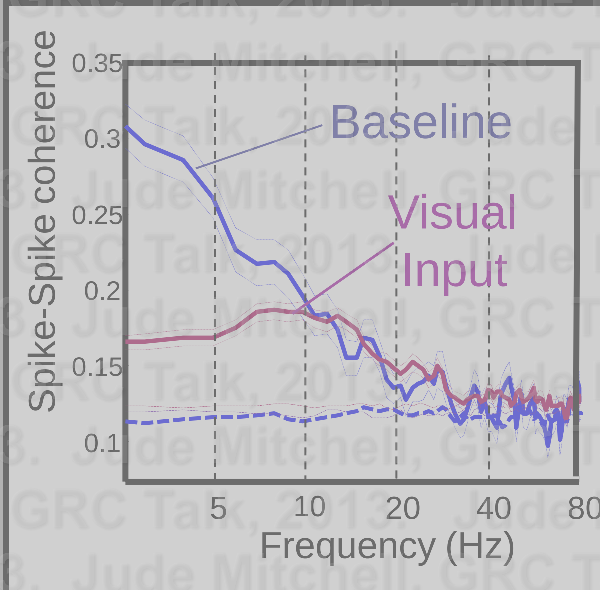
## Why does visual input reduce ongoing activity?

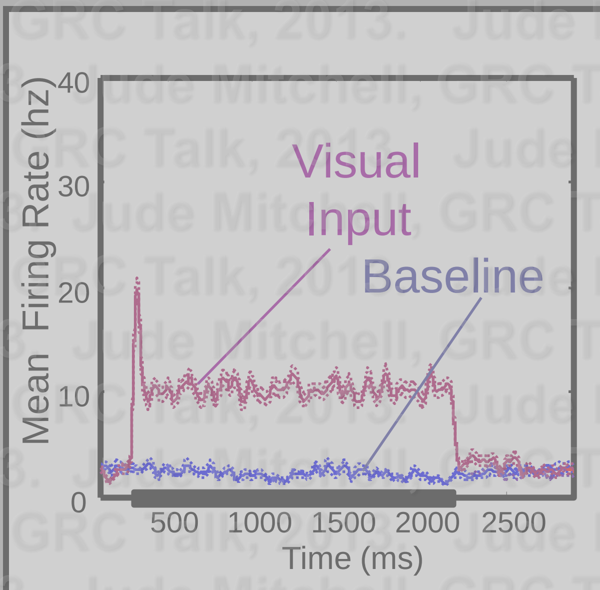
$$\tau \; dV/dt = g_{FF}\,(E_{FF} - V) + g_{REC}\,(E_{REC} - V)$$

$$V_{\infty} \cong \frac{g_{FF}\,E_{FF} + g_{REC}\,E_{REC}}{g_{FF} + g_{REC}}$$

Normalization = Weighted Averaging
Feed-forward vs Recurrent Terms

Reductions in spontaneous fluctuations are due to conductance clamping, not rate increases.



# Sensory input reduces ongoing activity

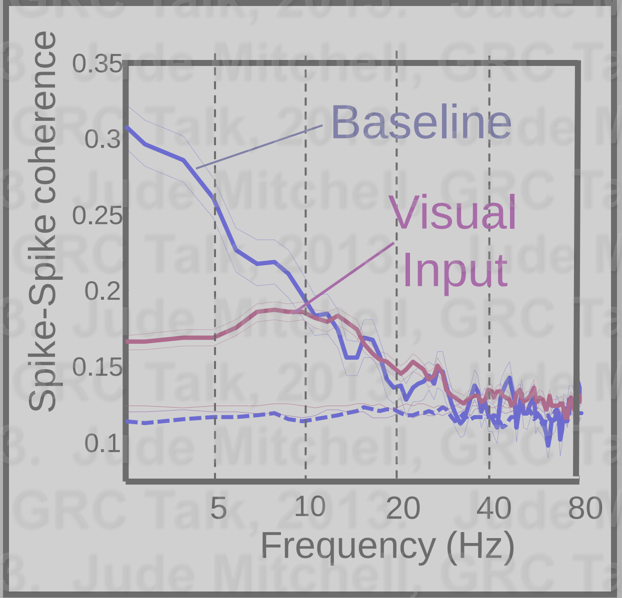
(Smith & Kohn, 2008; Churchland et al, 2009)

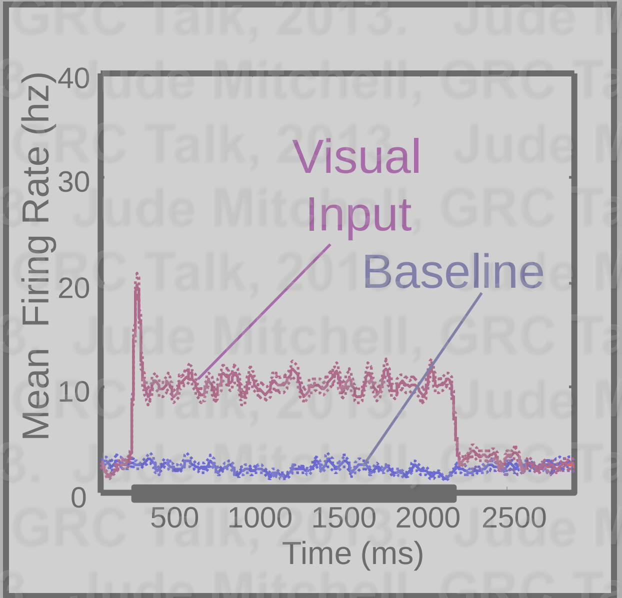
## Why does visual input reduce ongoing activity?

$$\tau \; dV/dt = g_{FF}(E_{FF} - V) + g_{REC}(E_{REC} - V)$$

$$V_{\infty} \cong \frac{g_{FF} E_{FF} + g_{REC} E_{REC}}{g_{FF} + g_{REC}}$$

Normalization = Weighted Averaging
Feed-forward vs Recurrent Terms

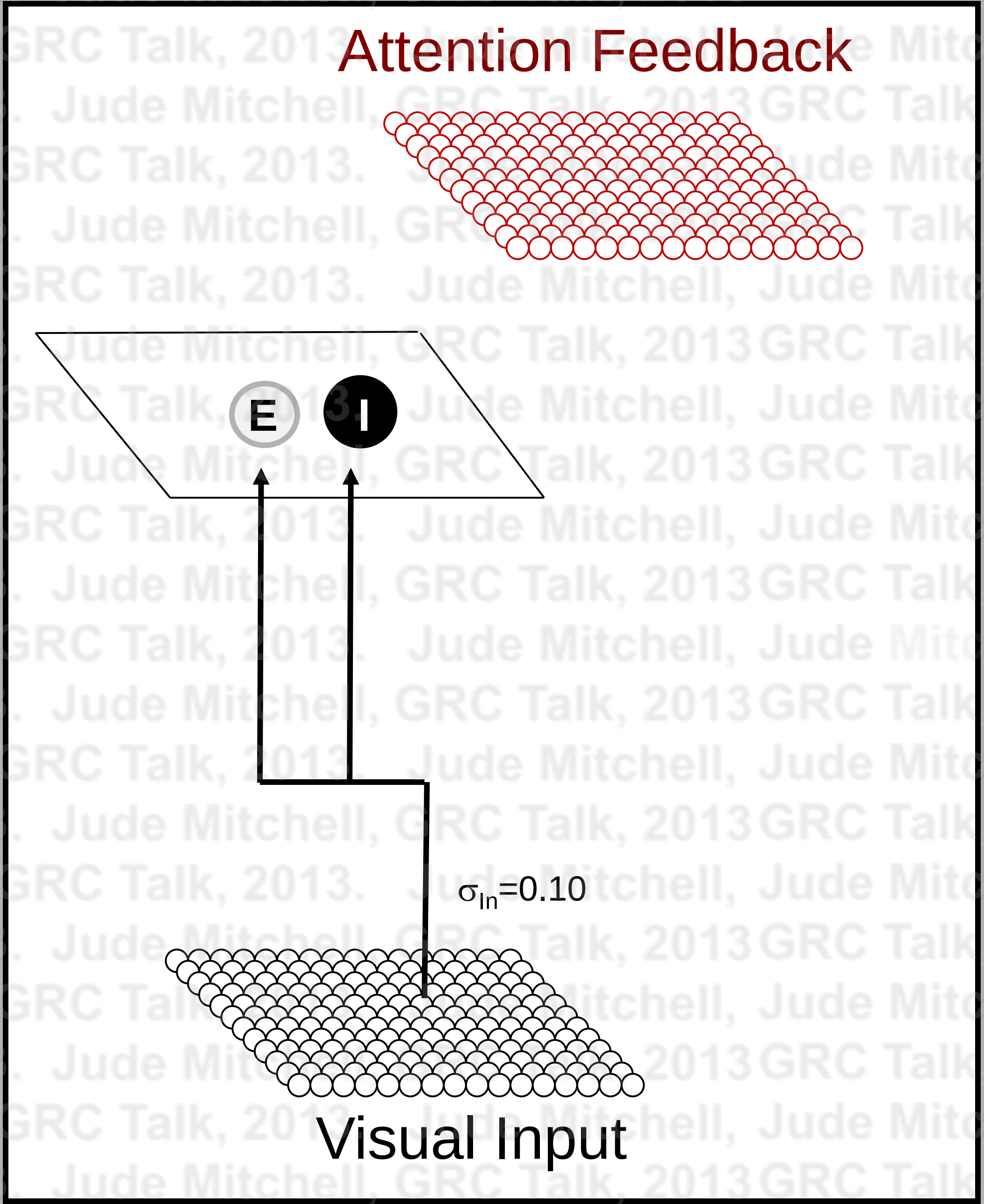


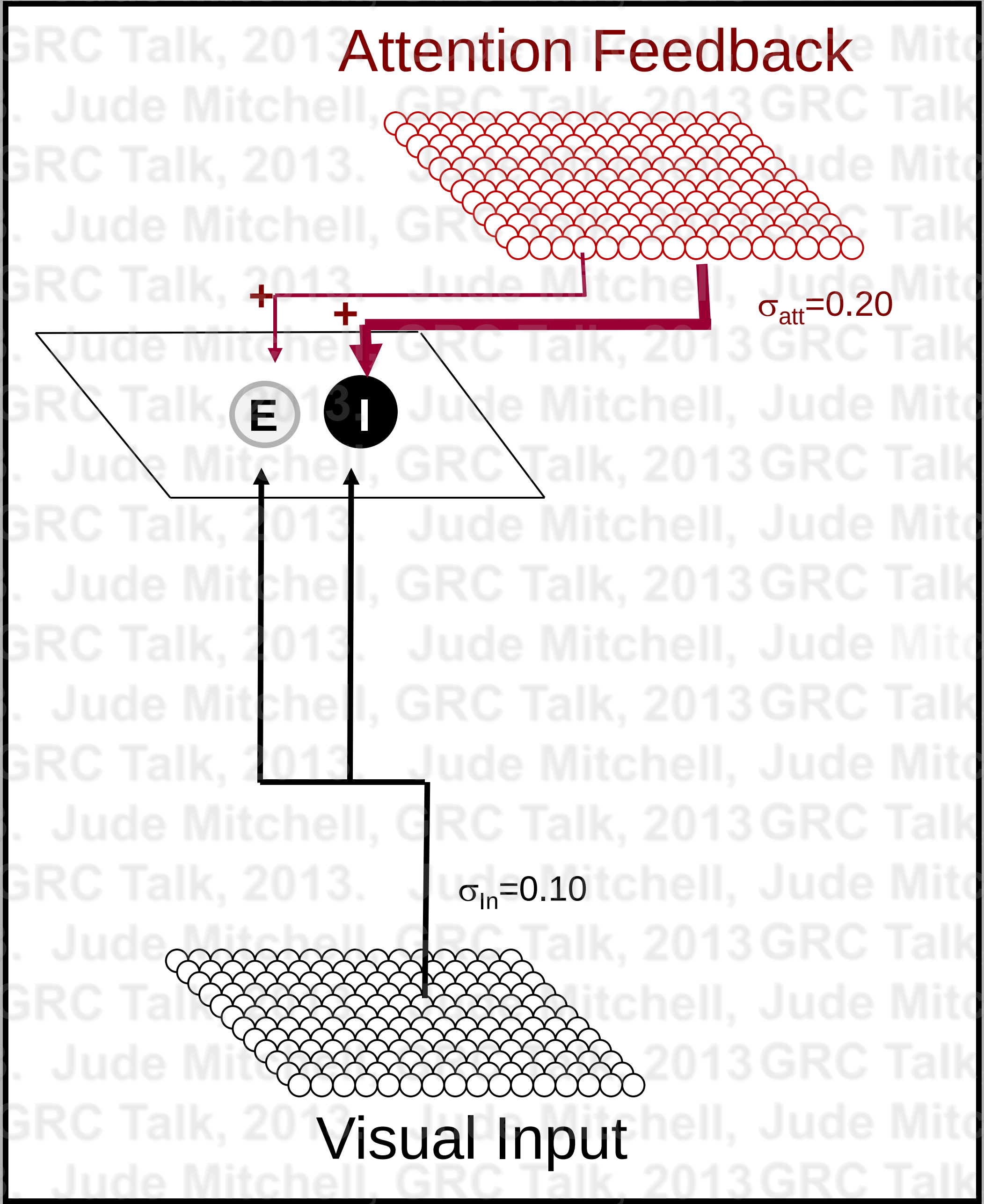

Reductions in spontaneous fluctuations are due to conductance clamping, not rate increases.

Prediction: **increased inhibition should also reduce fluctuations!**

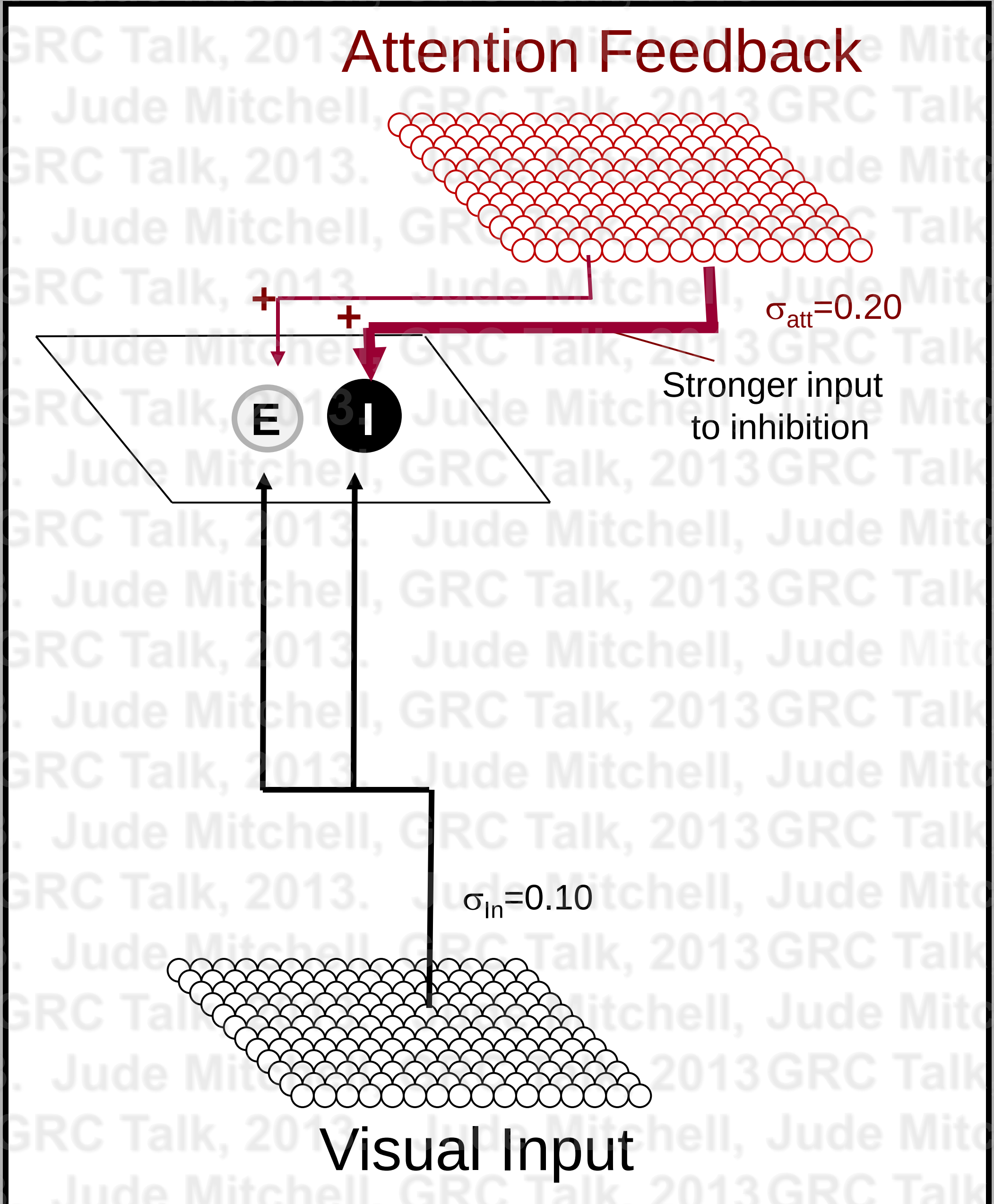
# Attention as local inhibition?



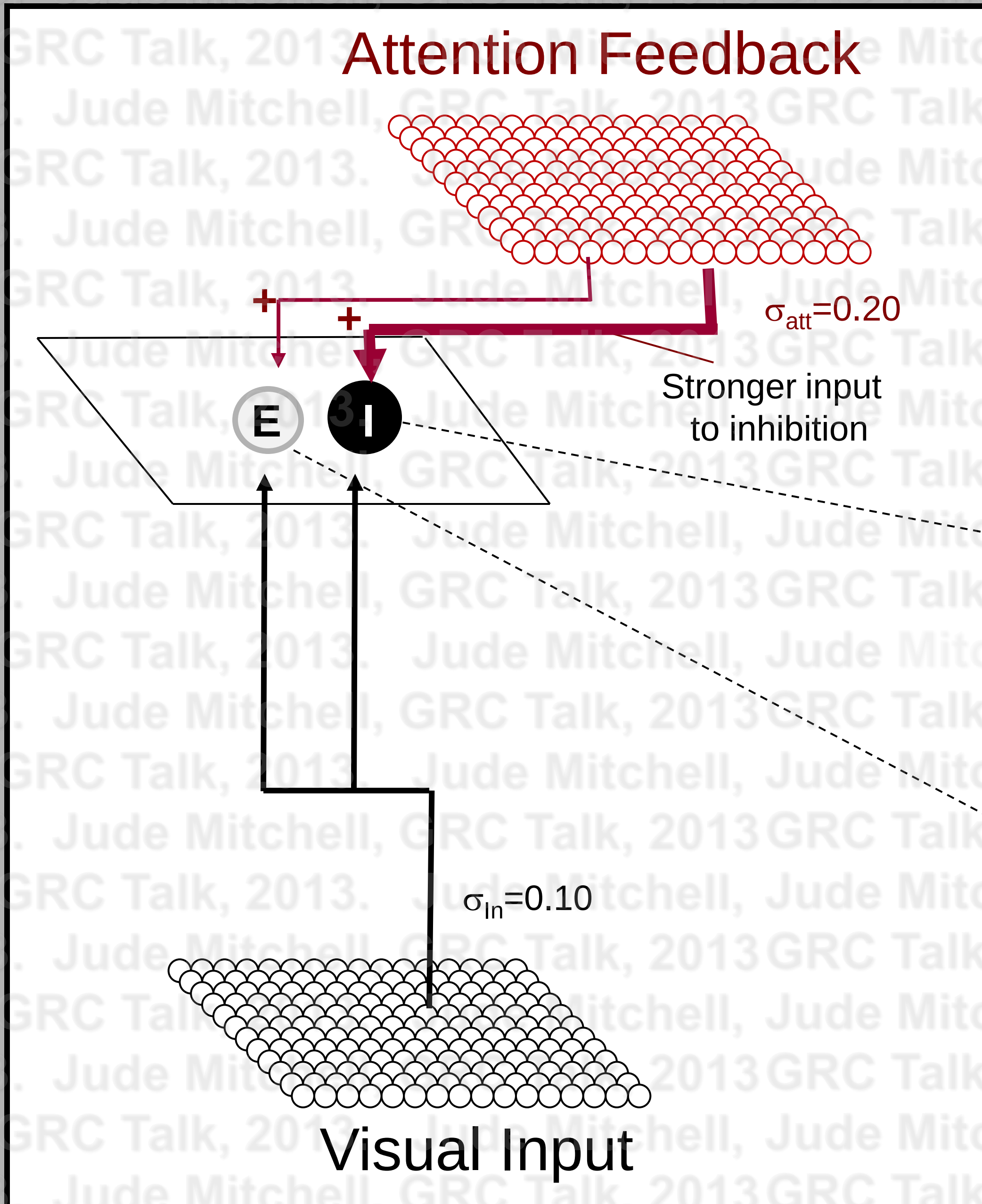
# Attention as local inhibition?

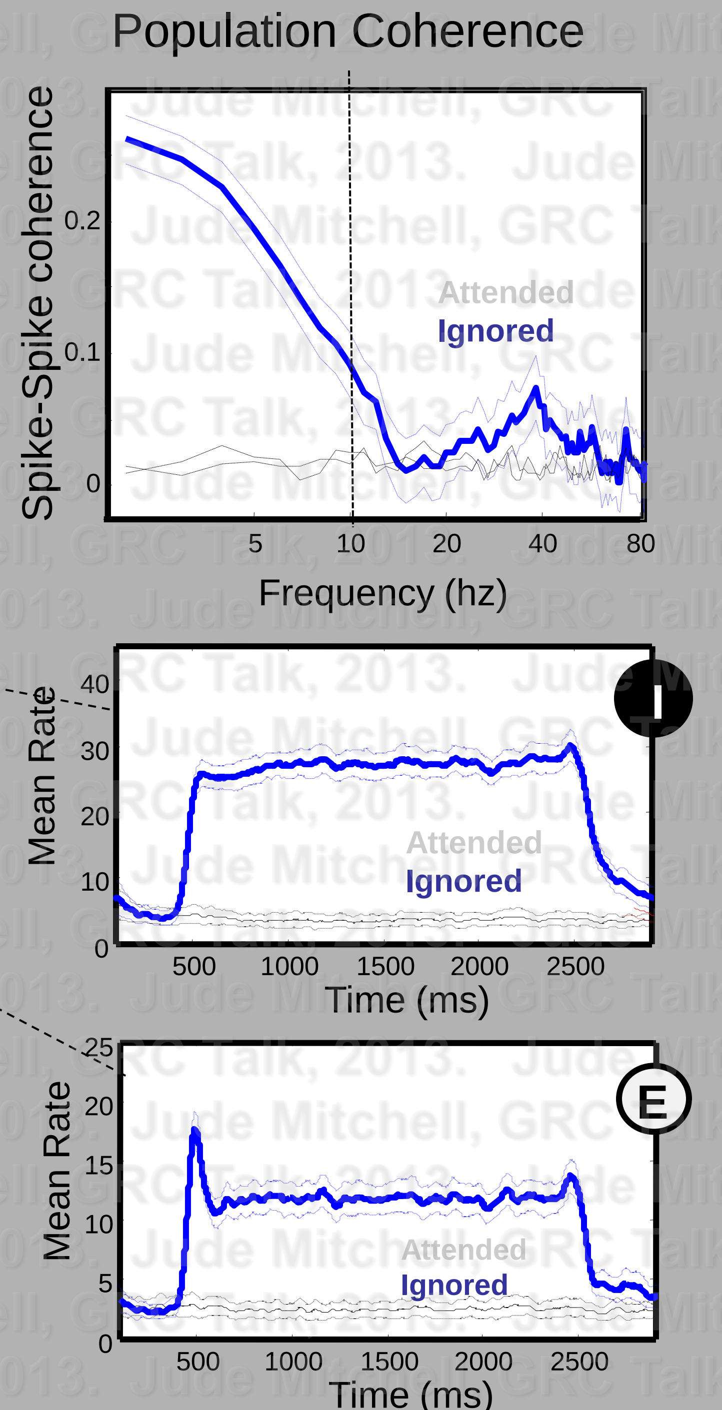


# Attention as local inhibition?

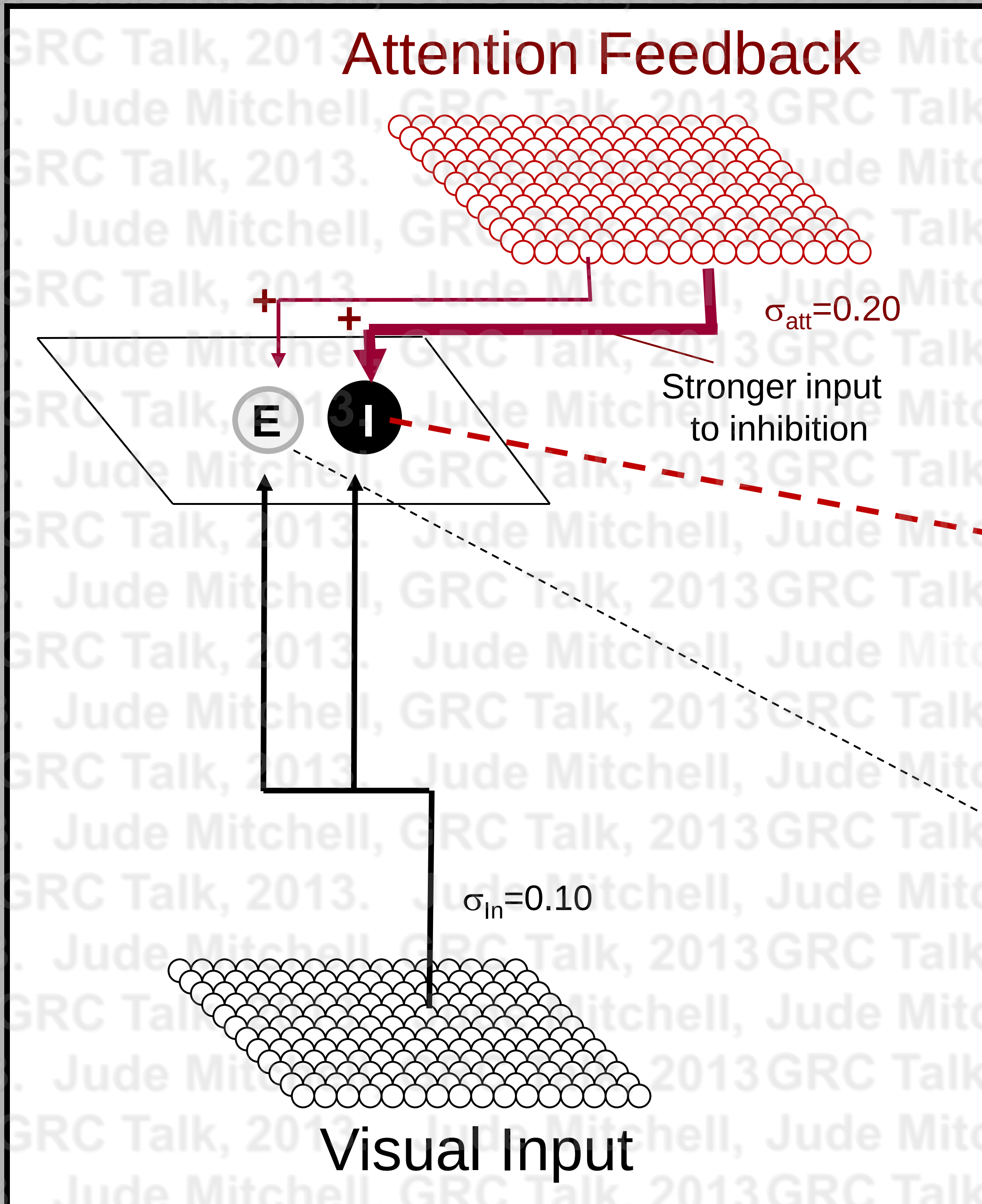


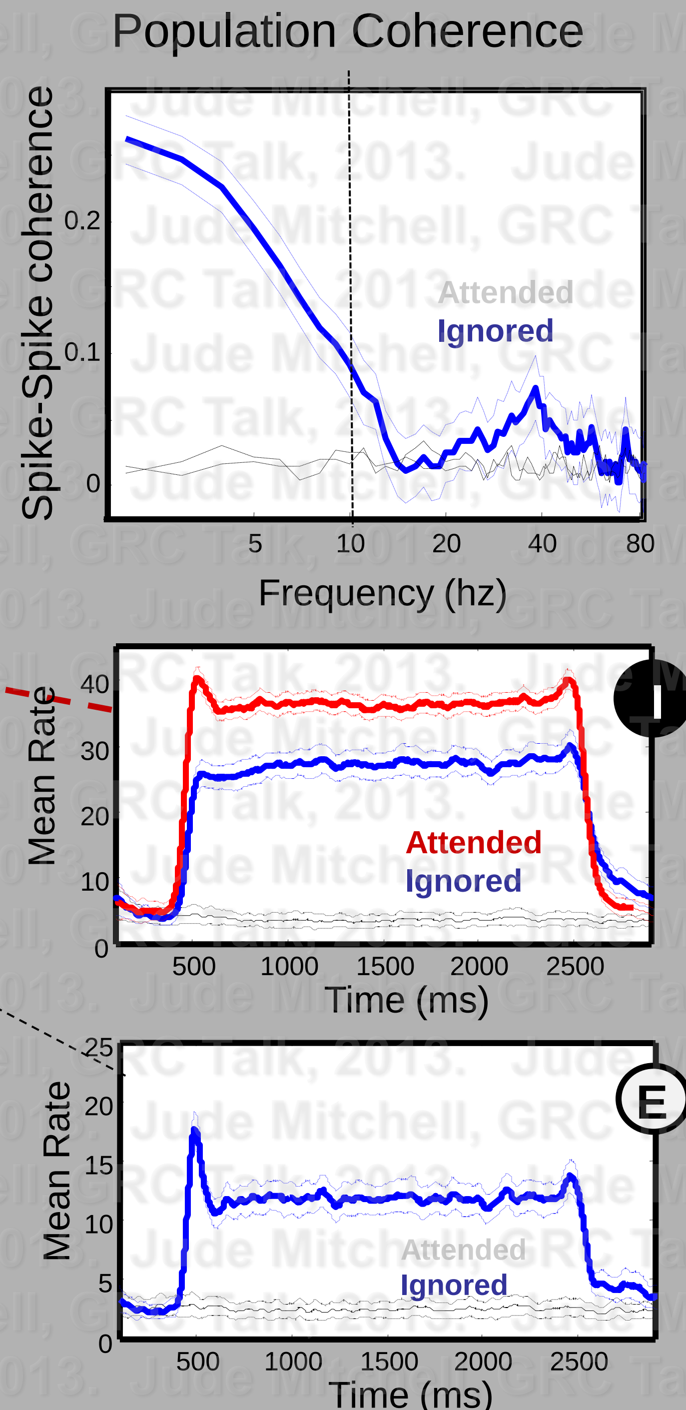
# Attention as local inhibition?



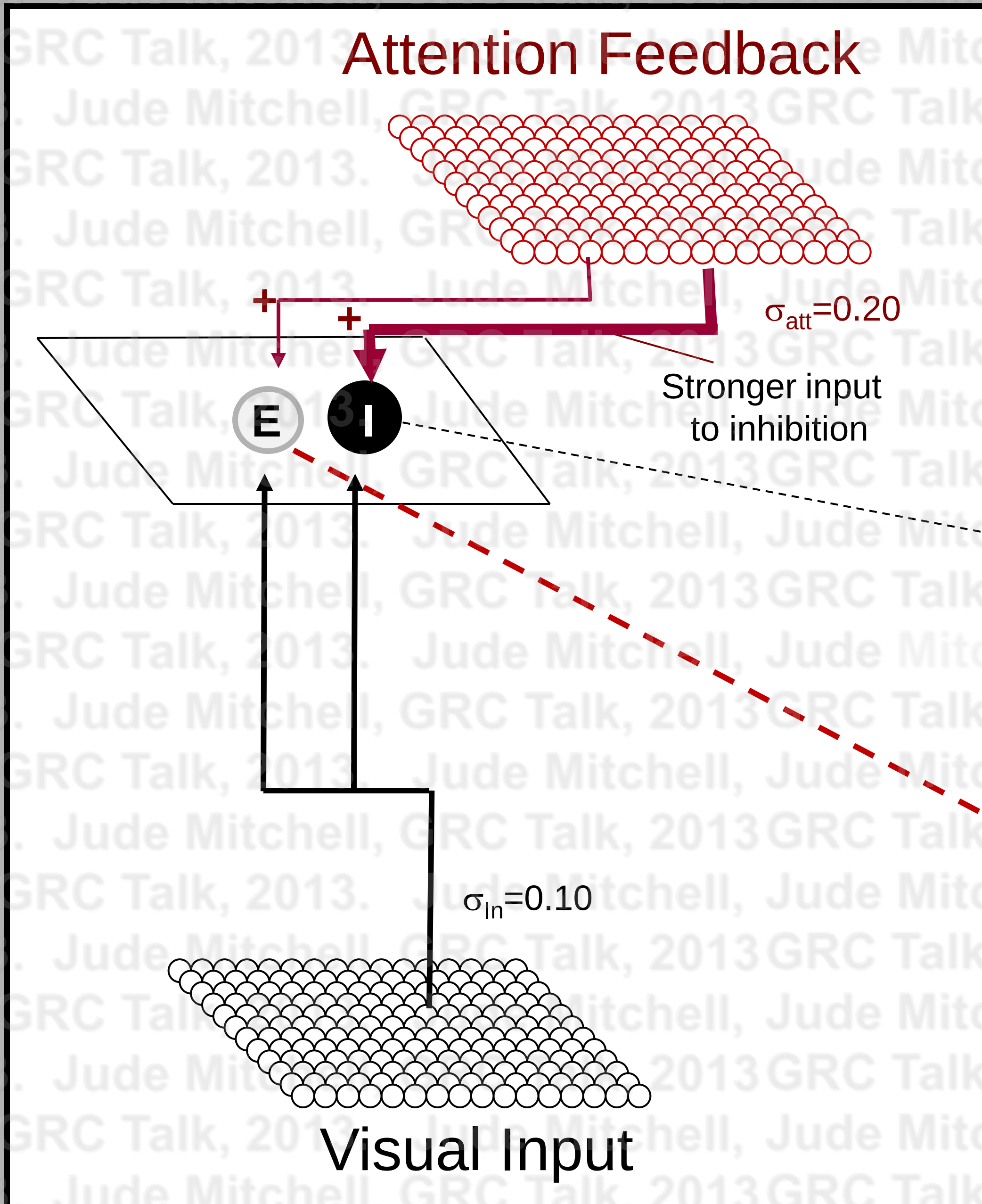



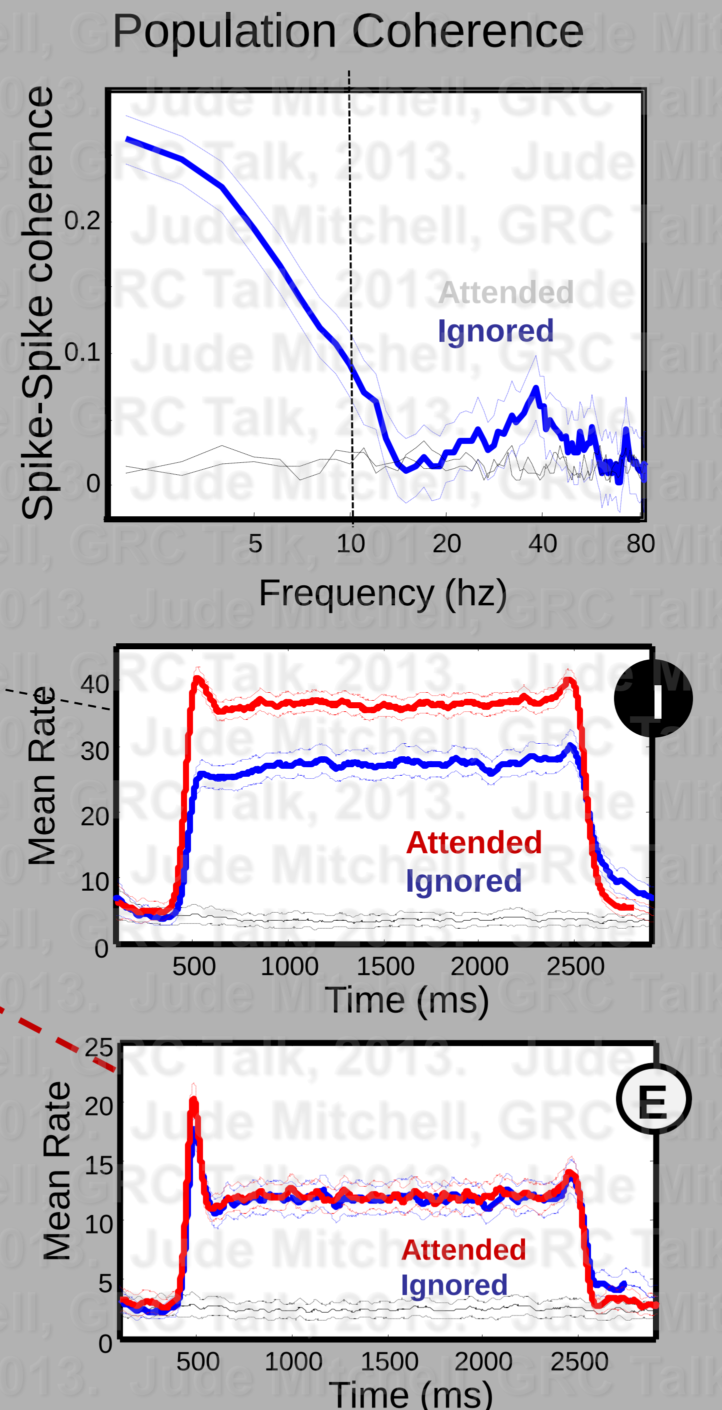
# Attention as local inhibition?



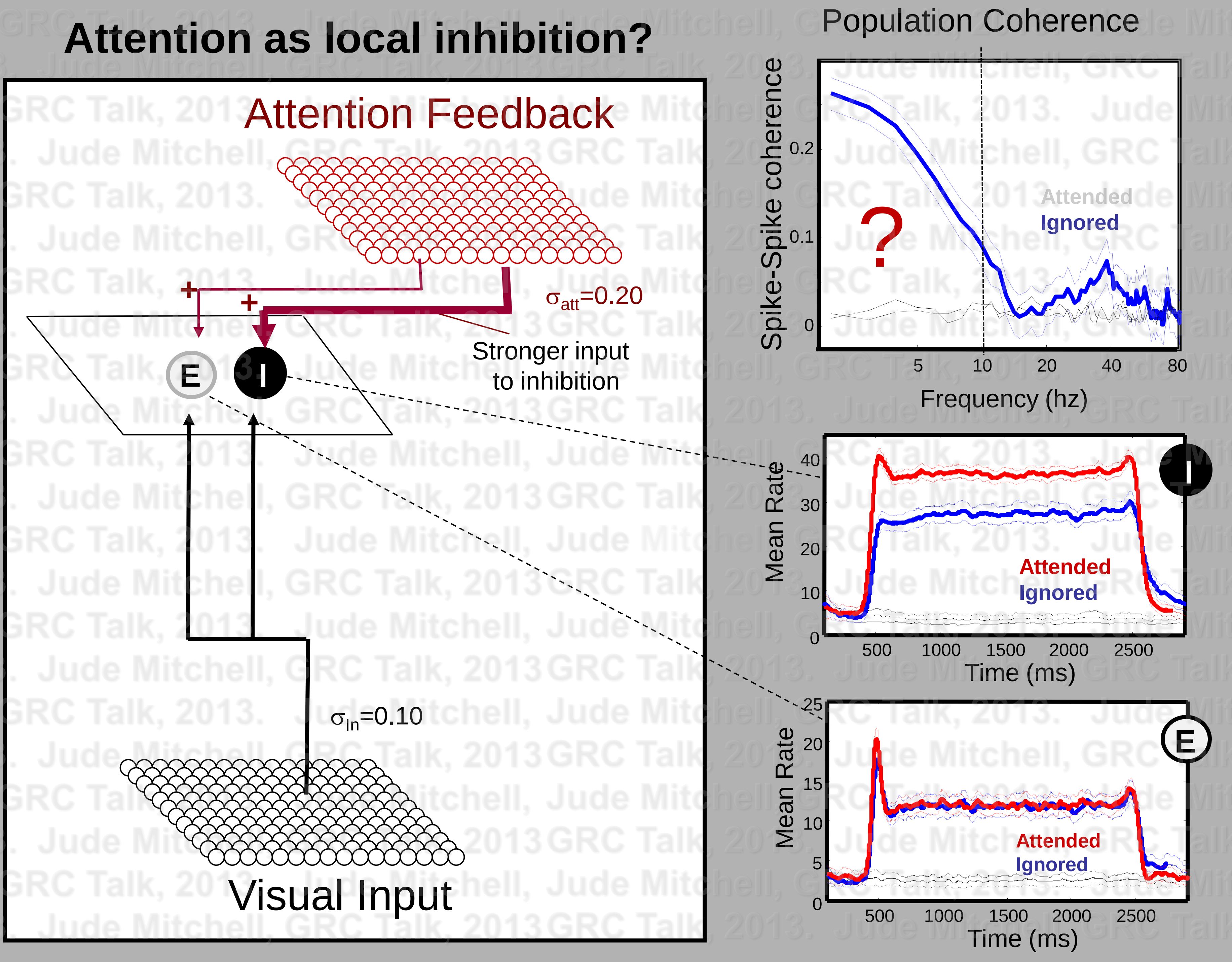



# Attention as local inhibition?

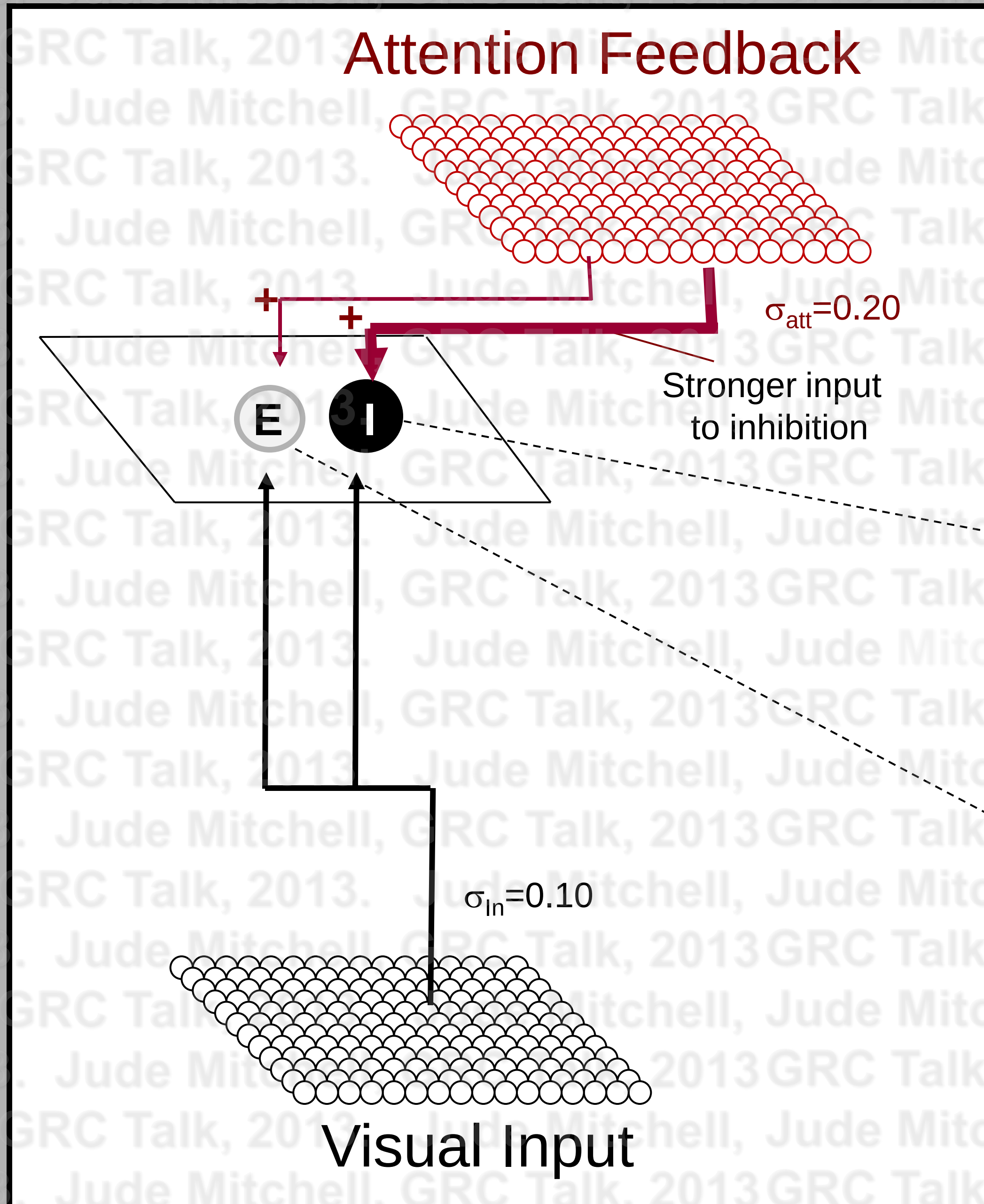


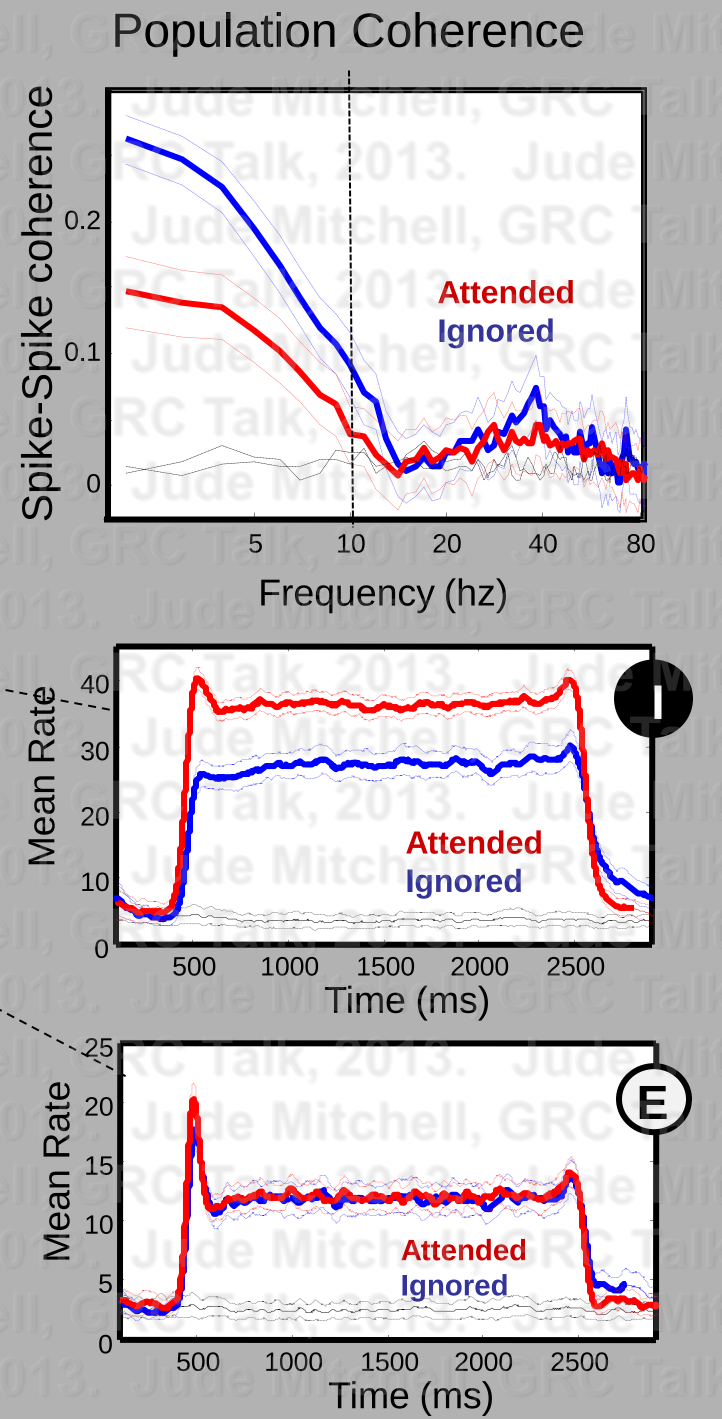



# Attention as local inhibition?



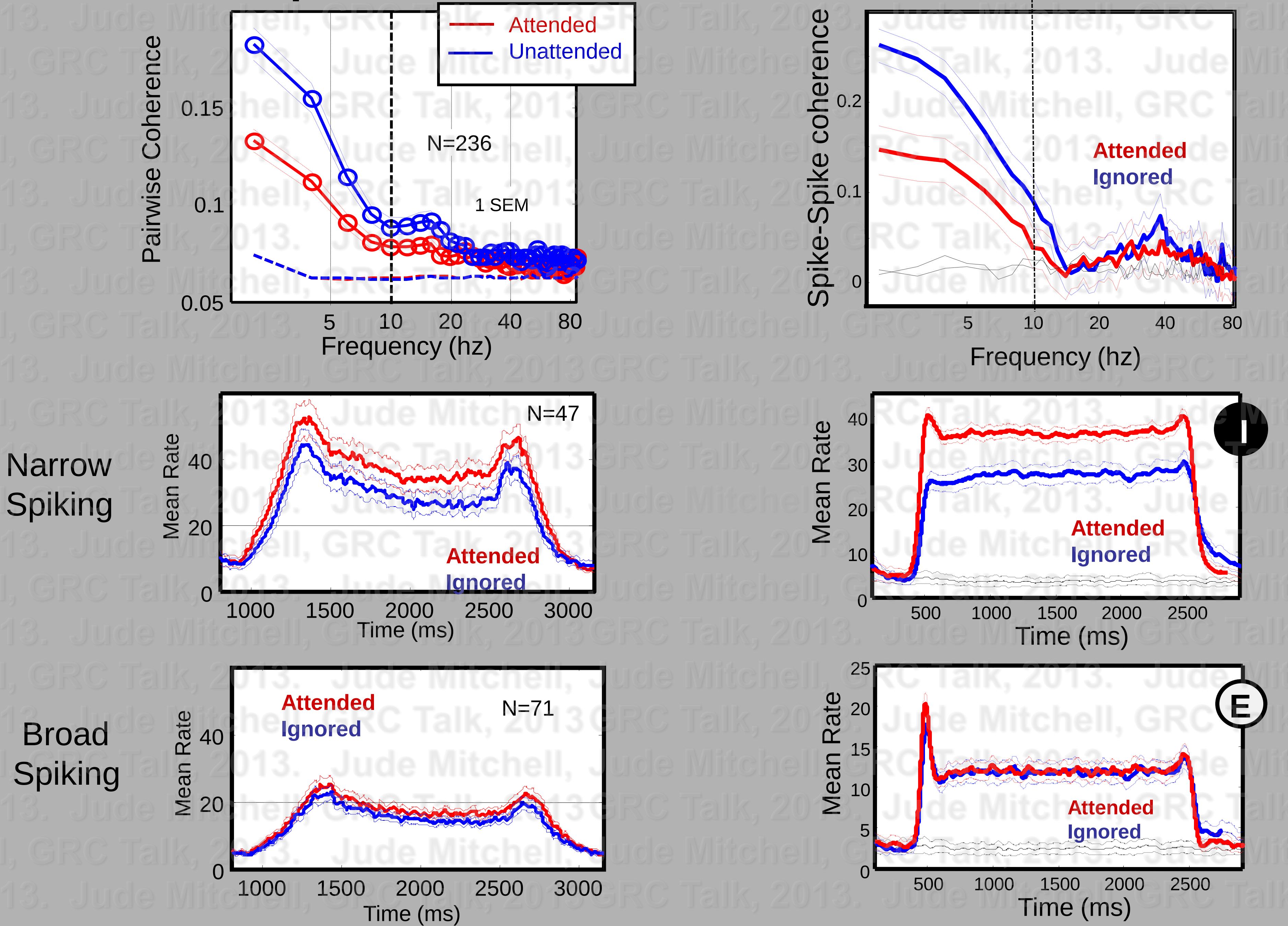
# Attention as local inhibition?



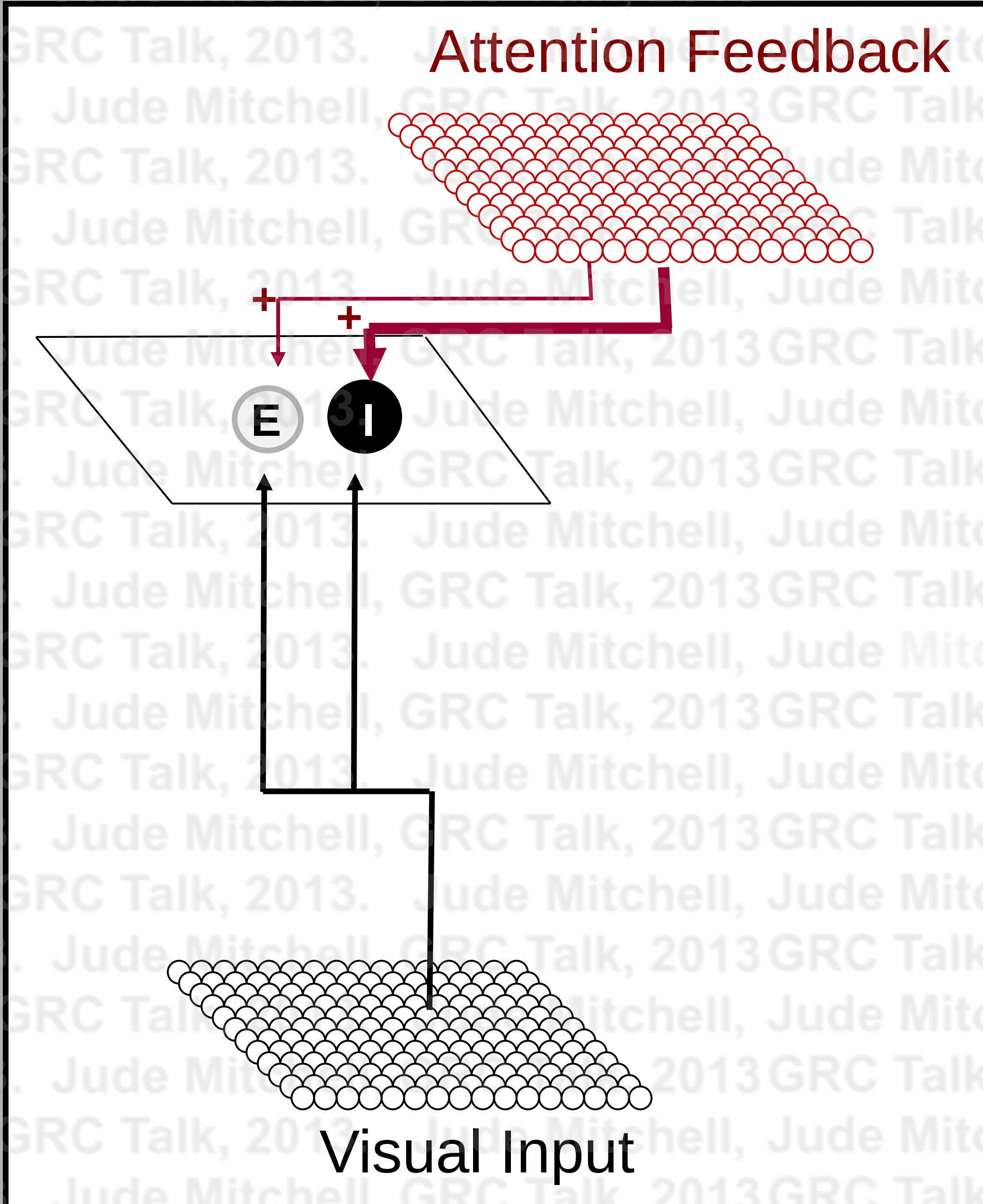



# Comparison to V4 Data

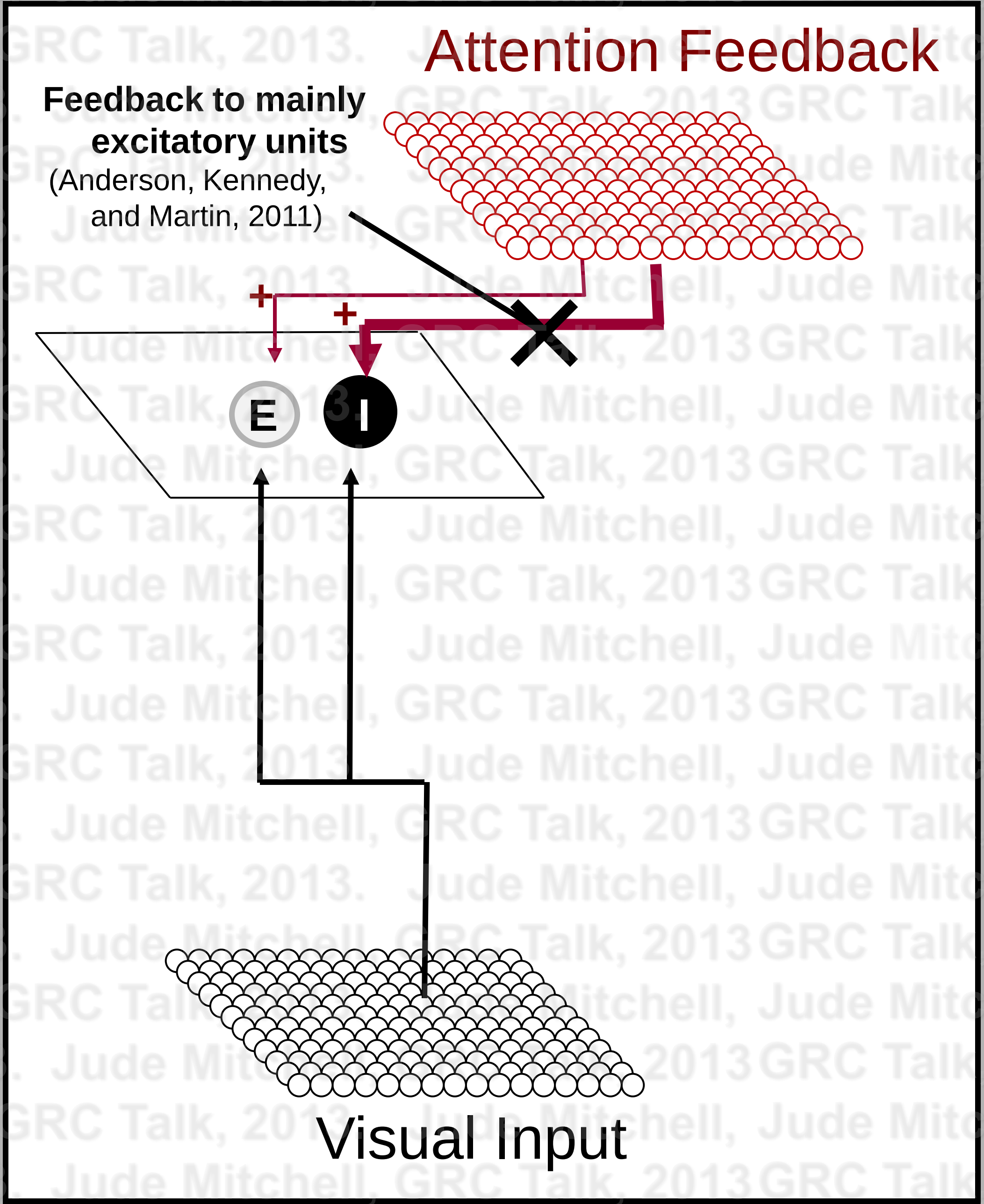
Population Coherence



# Model predictions?

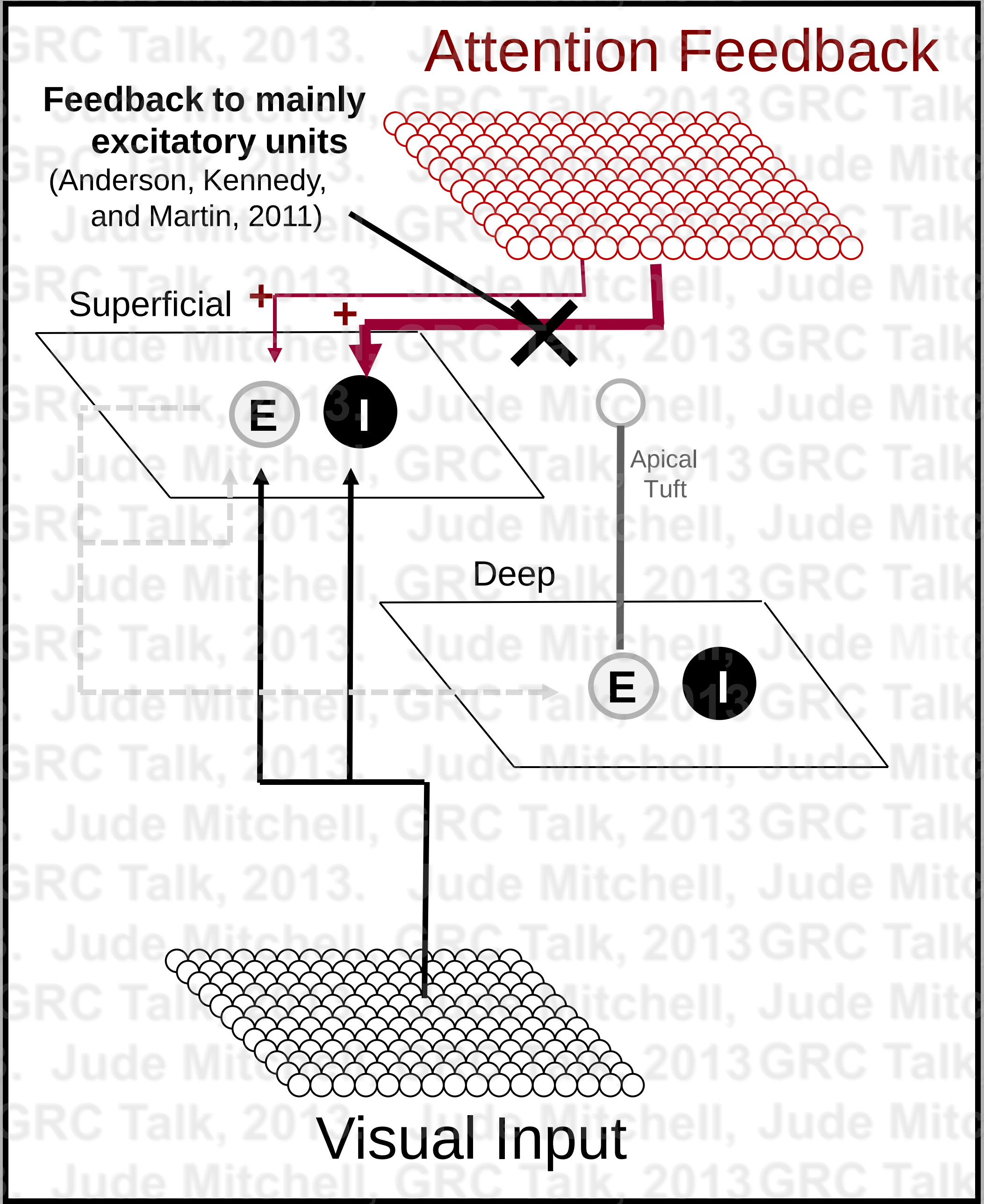


# Model predictions?



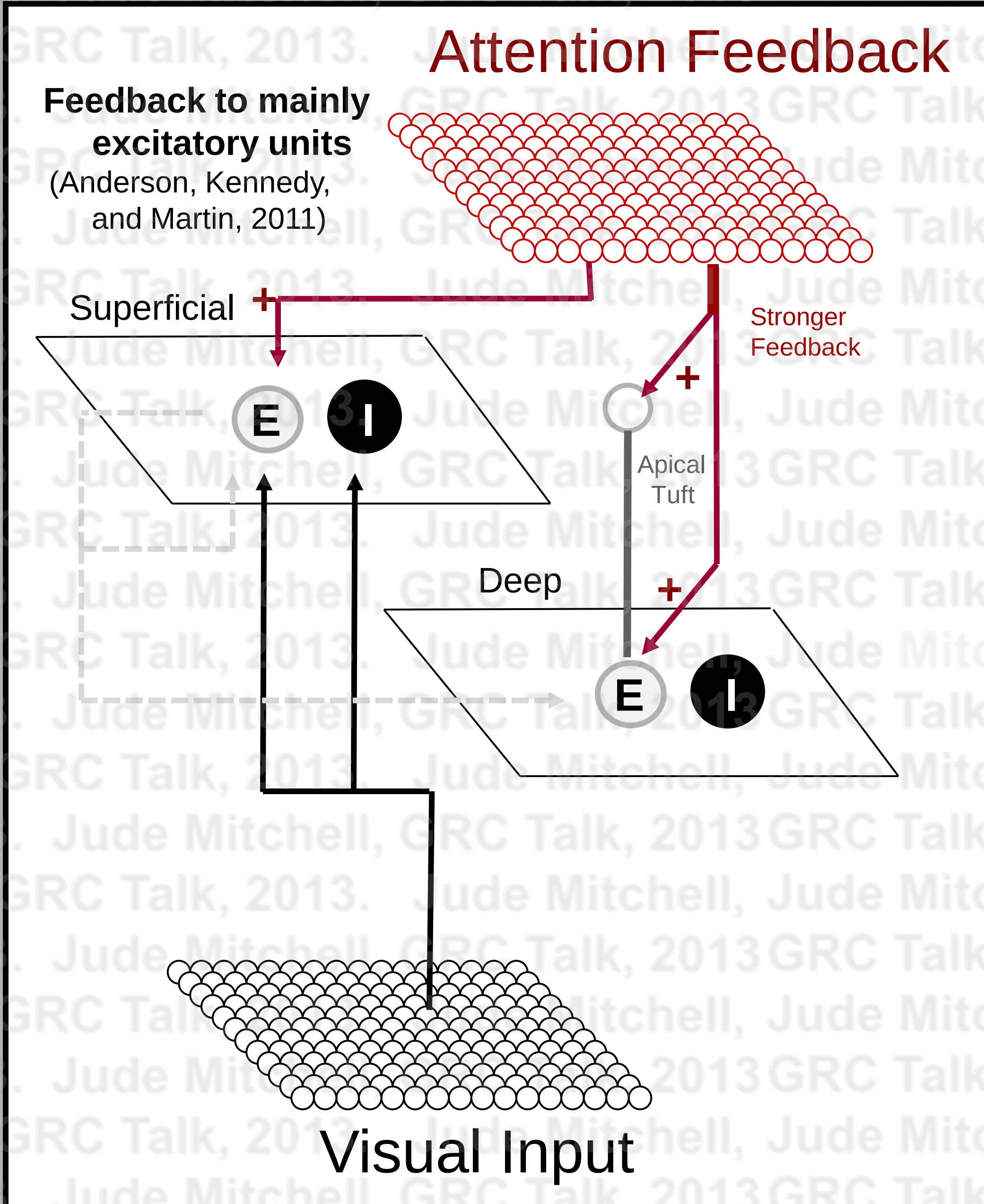
Laminar Model

# Model predictions?



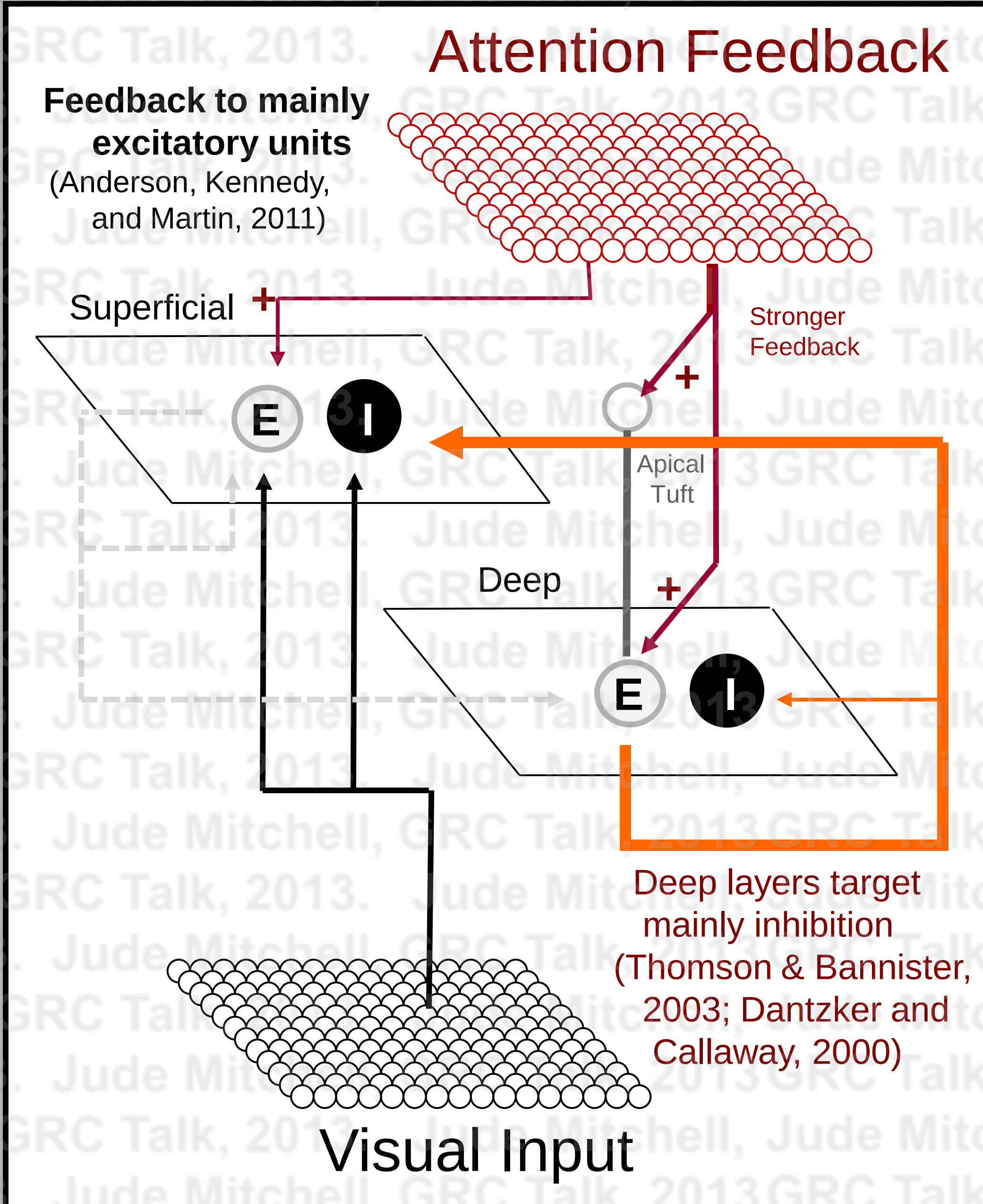
Laminar Model

# Model predictions?

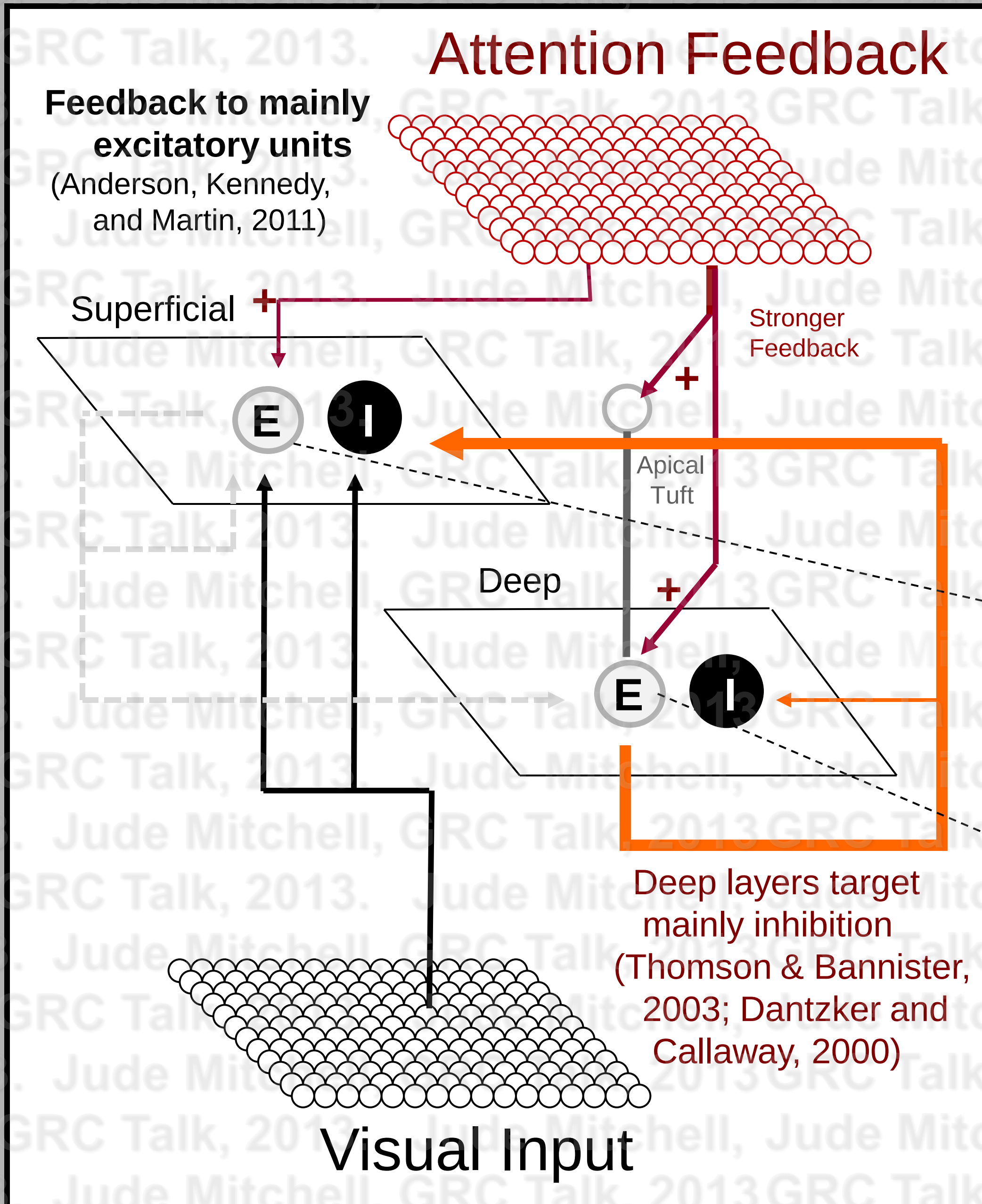


Laminar Model

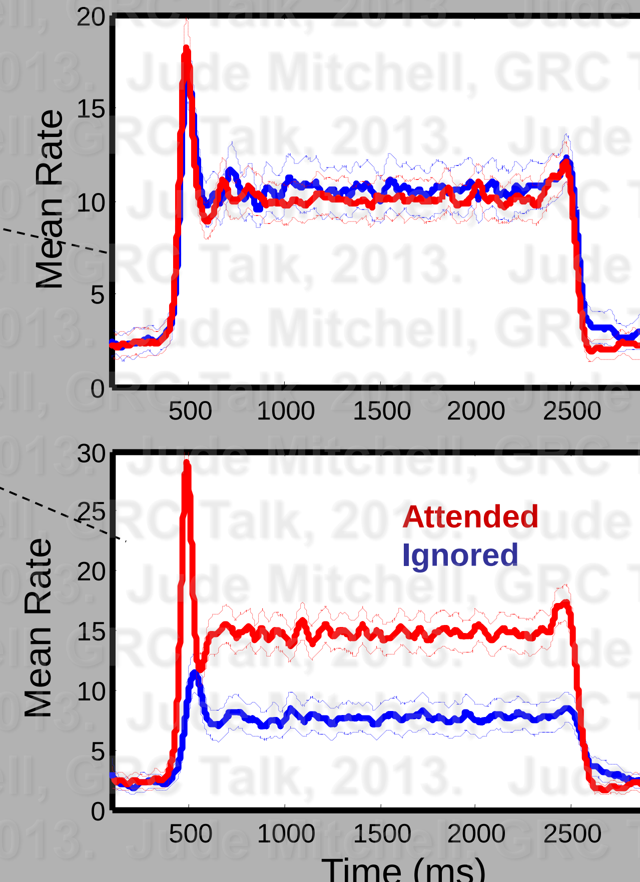
# Model predictions?



# Laminar Model



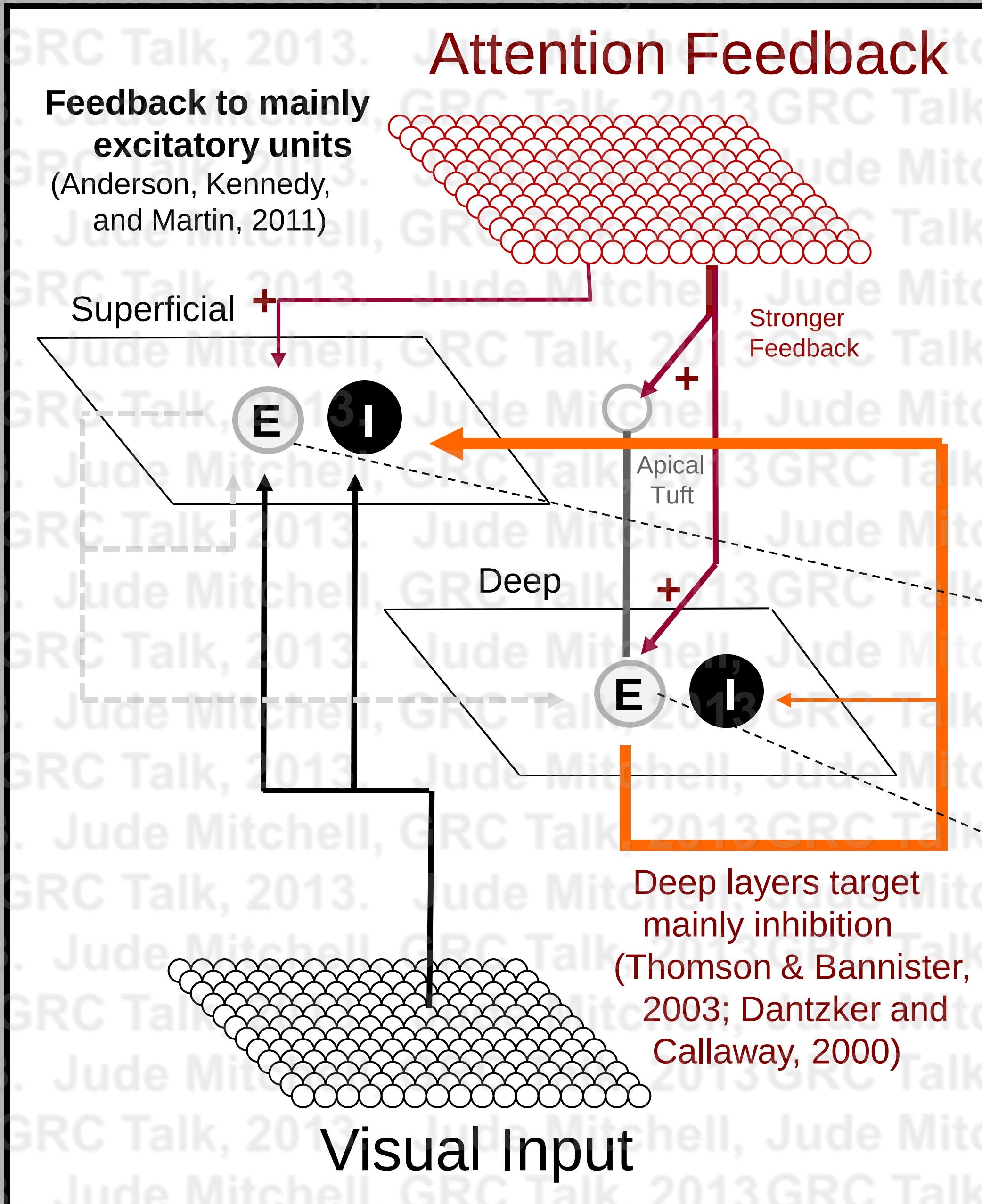

# Model predictions?

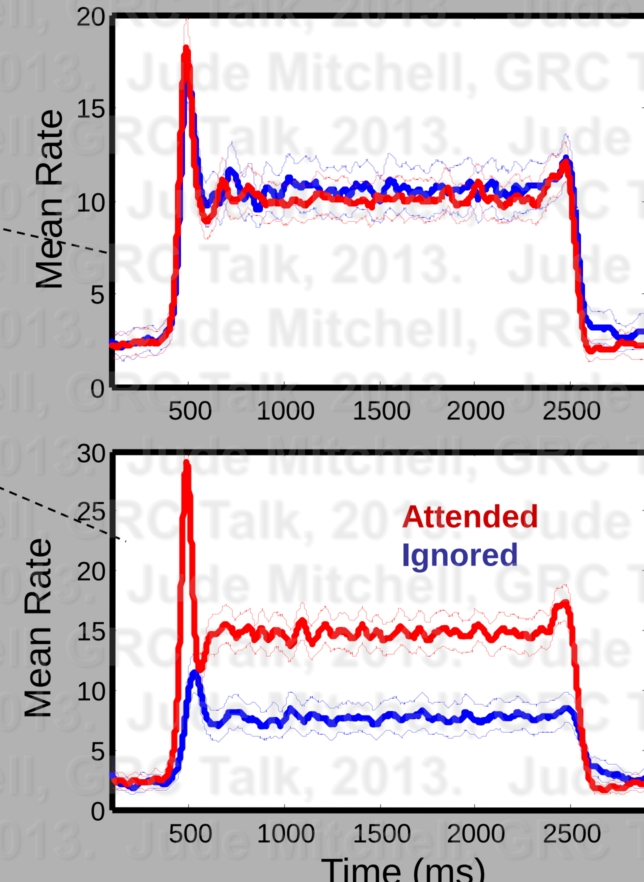


Laminar Model

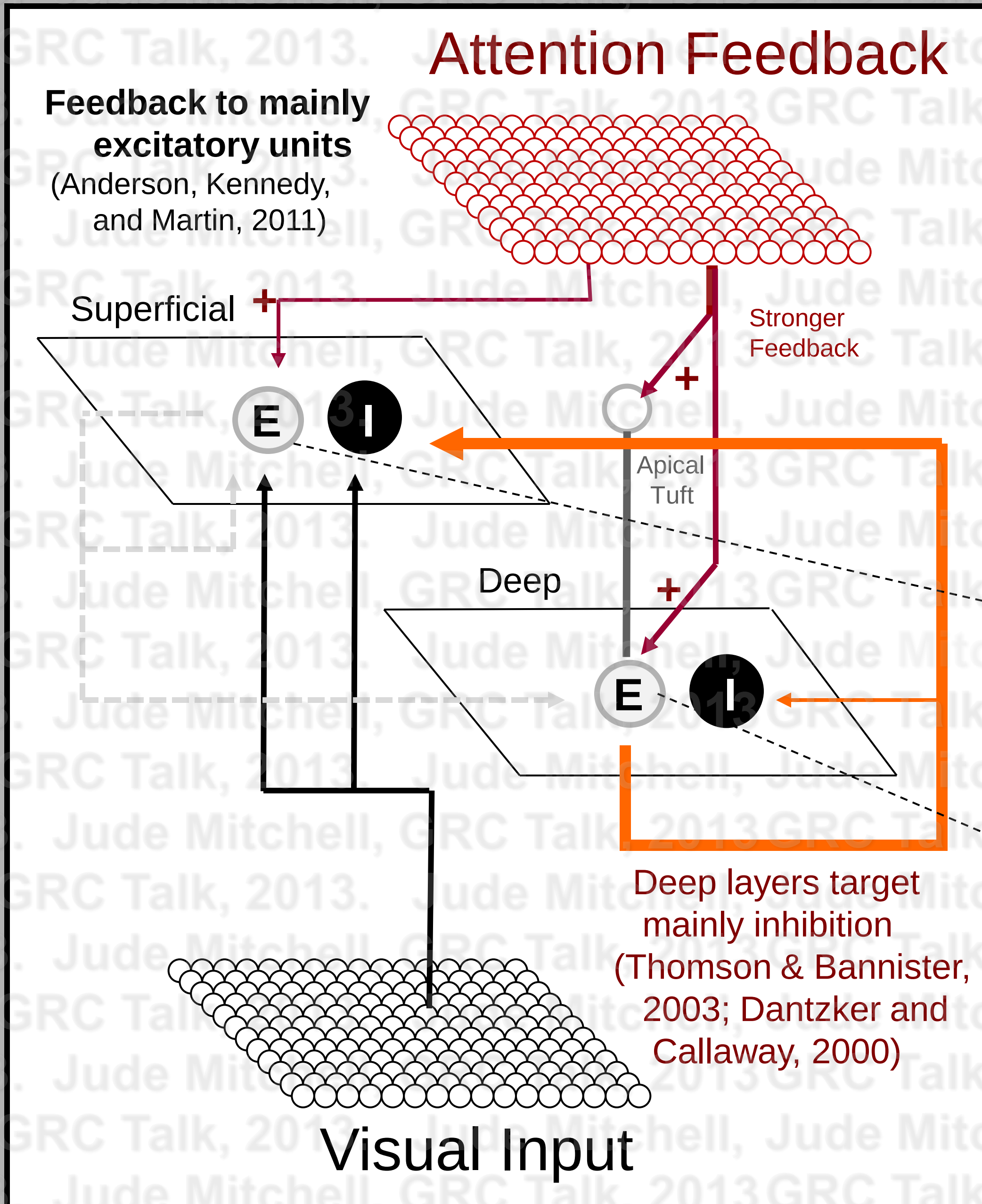
# Model predictions?

- deep layers show greater modulation



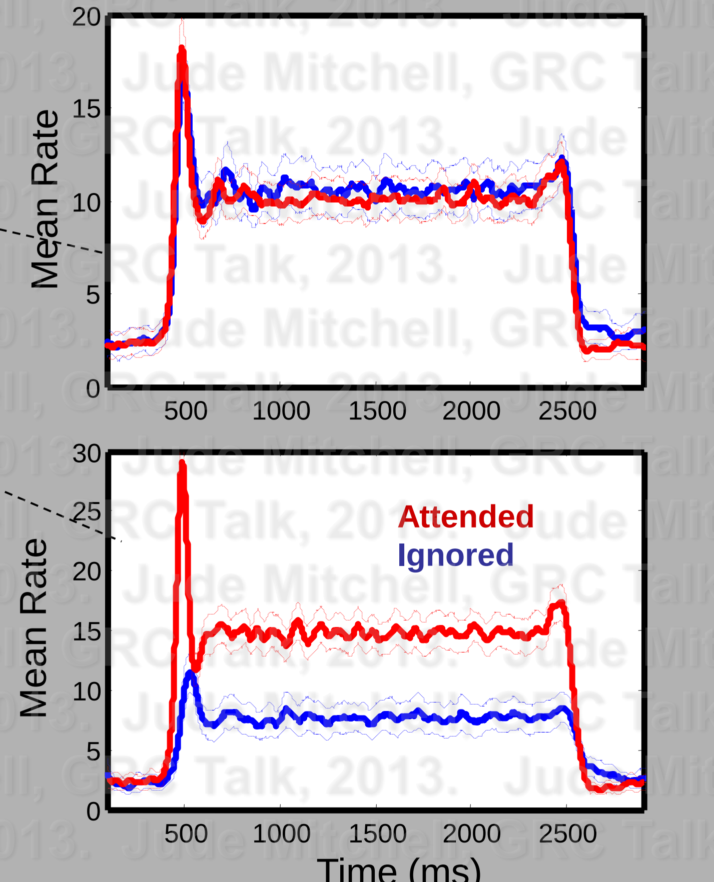
Laminar Model




# Model predictions?

- deep layers show greater modulation

Burst firing pyramids show larger gain increases
**(Anderson, Mitchell, Reynolds, J. Neuroscience, 2011)**

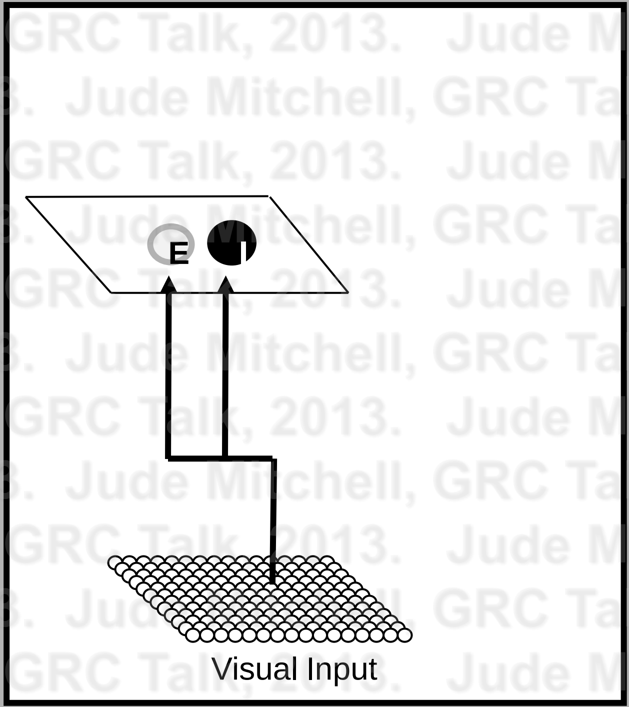


# Summary:

Recurrent networks in a balanced regime
exhibit correlated fluctuations

Feed-forward inputs clamp activity
reducing those fluctuations

Inhibition also clamps out fluctuations



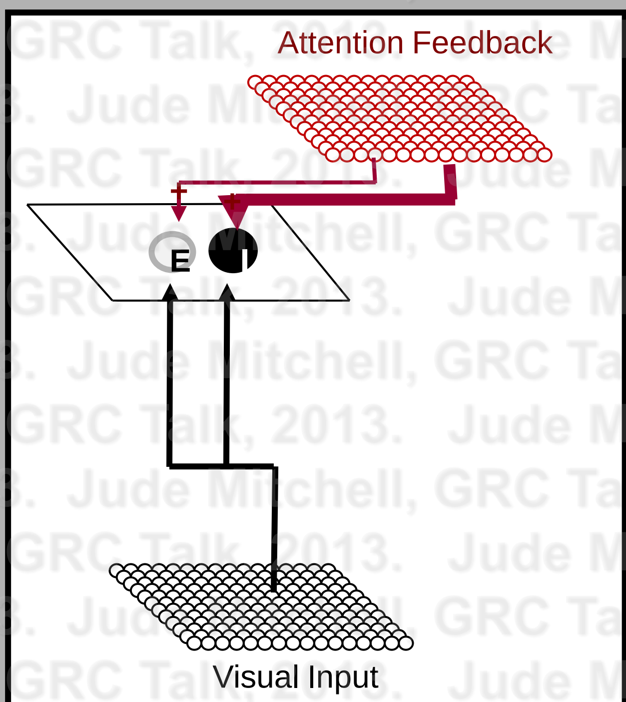

(Mitchell and Reynolds, *in prep*)

# Summary:

Recurrent networks in a balanced regime exhibit correlated fluctuations

Feed-forward inputs clamp activity reducing those fluctuations

Inhibition also clamps out fluctuations




(Mitchell and Reynolds, *in prep*)

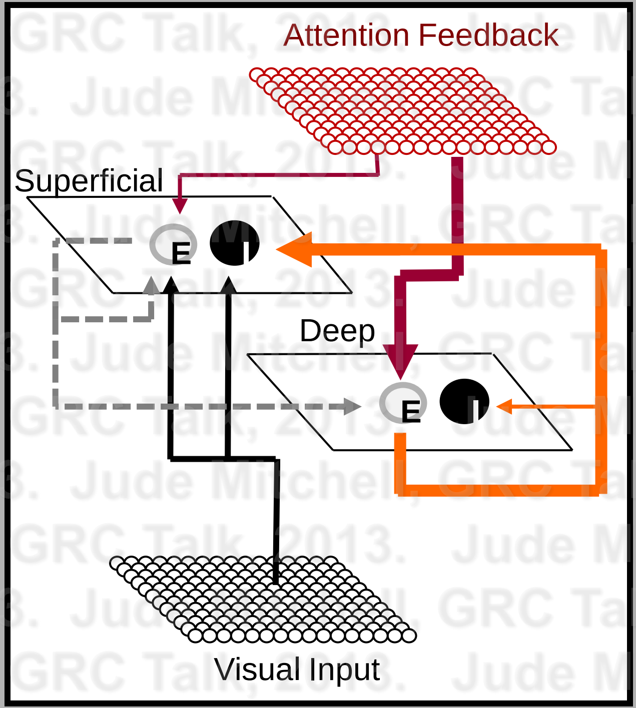
Attention clamps ongoing activity by increasing local inhibition

# Summary:

Recurrent networks in a balanced regime
exhibit correlated fluctuations

Feed-forward inputs clamp activity
reducing those fluctuations

Inhibition also clamps out fluctuations




Attention clamps ongoing activity
by increasing local inhibition

Prediction: deep layers increase
gain more than superficial layers

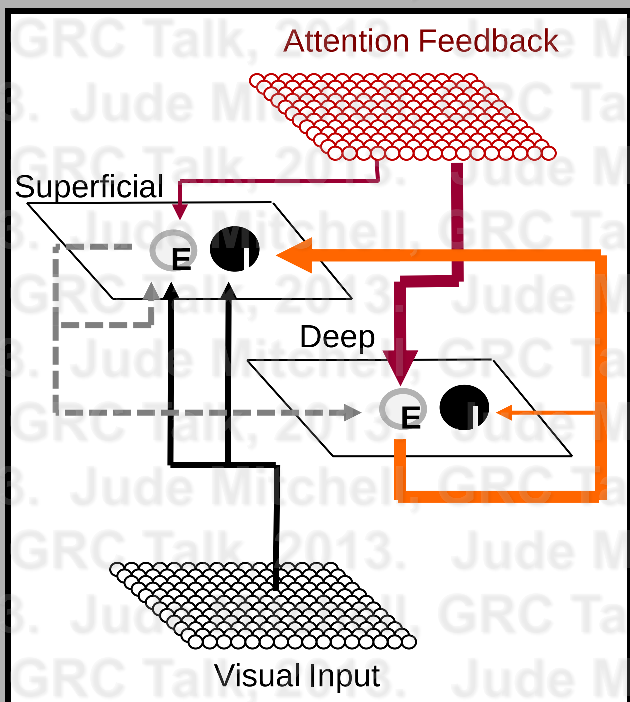
(Mitchell and Reynolds, *in prep*)

# Summary:

Recurrent networks in a balanced regime
exhibit correlated fluctuations

Feed-forward inputs clamp activity
reducing those fluctuations

Inhibition also clamps out fluctuations




(Mitchell and Reynolds, *in prep*)

Attention clamps ongoing activity
by increasing local inhibition

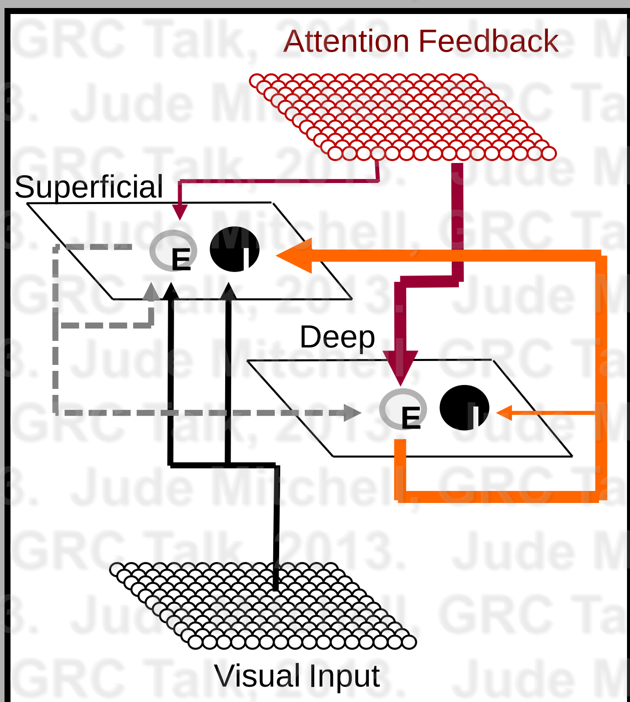
Prediction: deep layers increase
gain more than superficial layers

# Summary:

Recurrent networks in a balanced regime exhibit correlated fluctuations

Feed-forward inputs clamp activity reducing those fluctuations

Inhibition also clamps out fluctuations




(Mitchell and Reynolds, *in prep*)

Attention clamps ongoing activity by increasing local inhibition

Prediction: deep layers increase gain more than superficial layers

Problems of macaque sulci

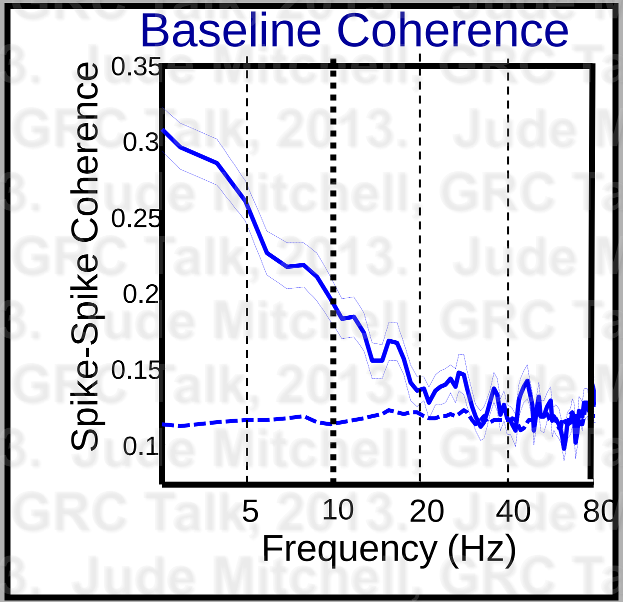

# Acknowledgments

John Reynolds

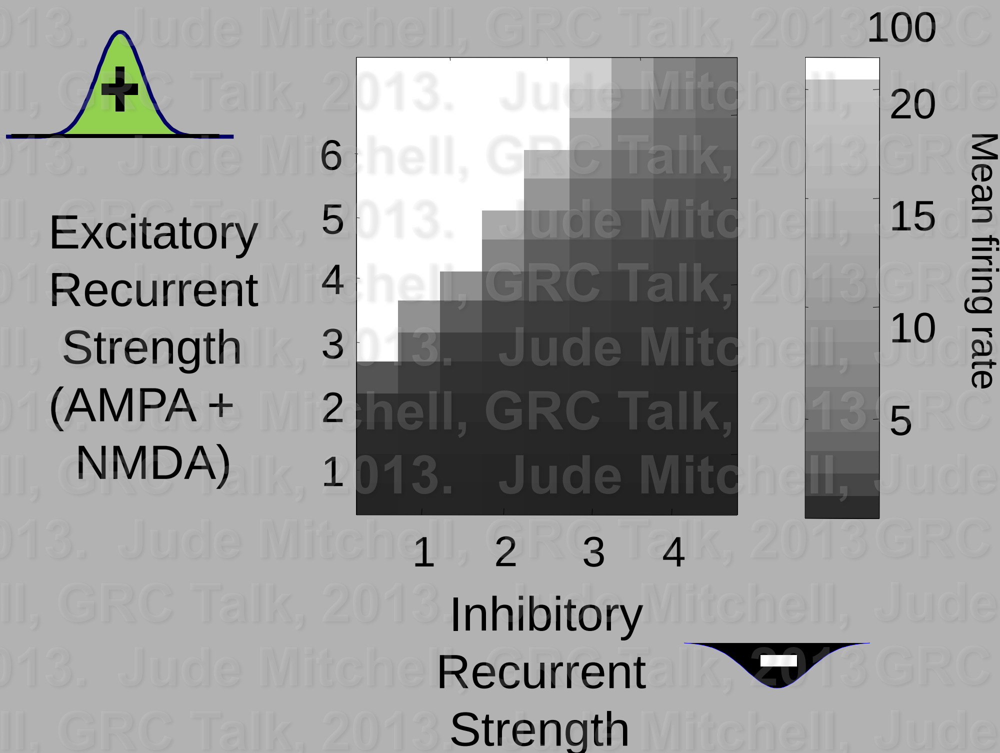
Funding:

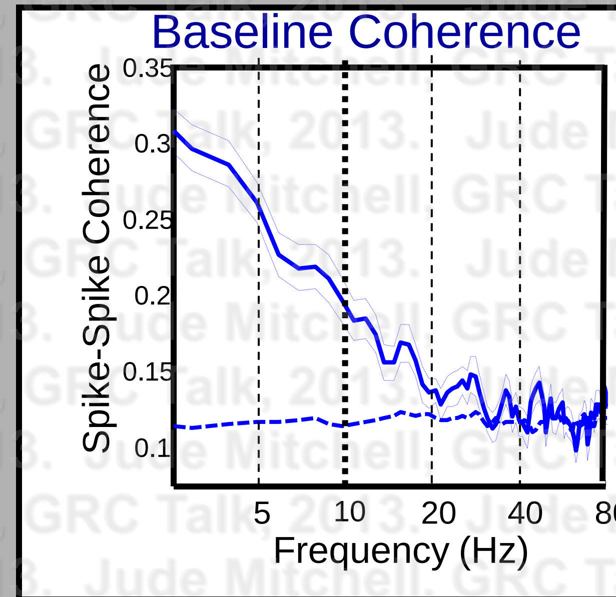
The Swartz Foundation for Computational Neuroscience

What model parameters are essential to the shared fluctuations?

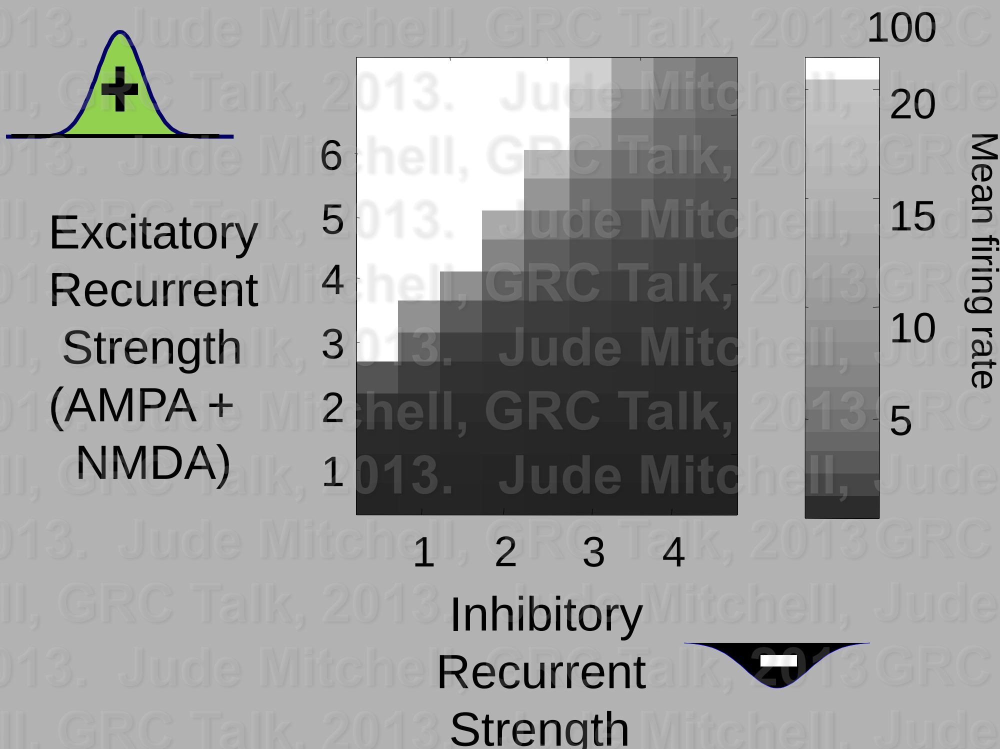


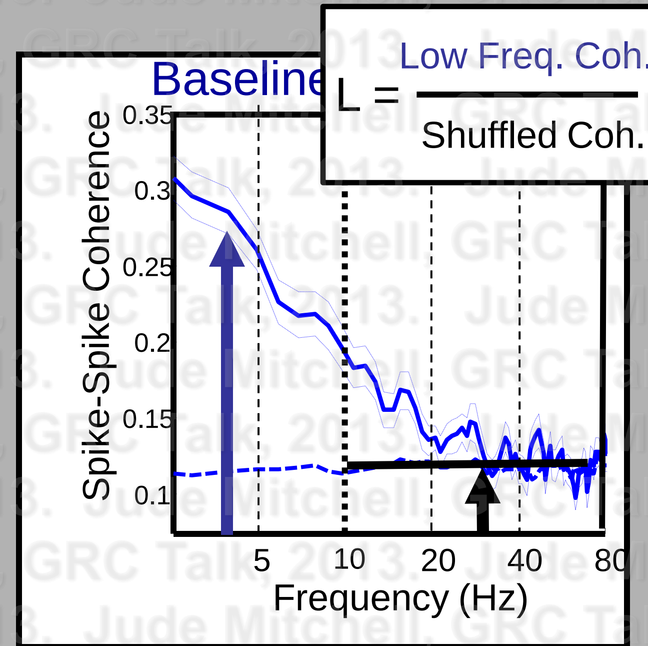
# What model parameters are essential to the shared fluctuations?



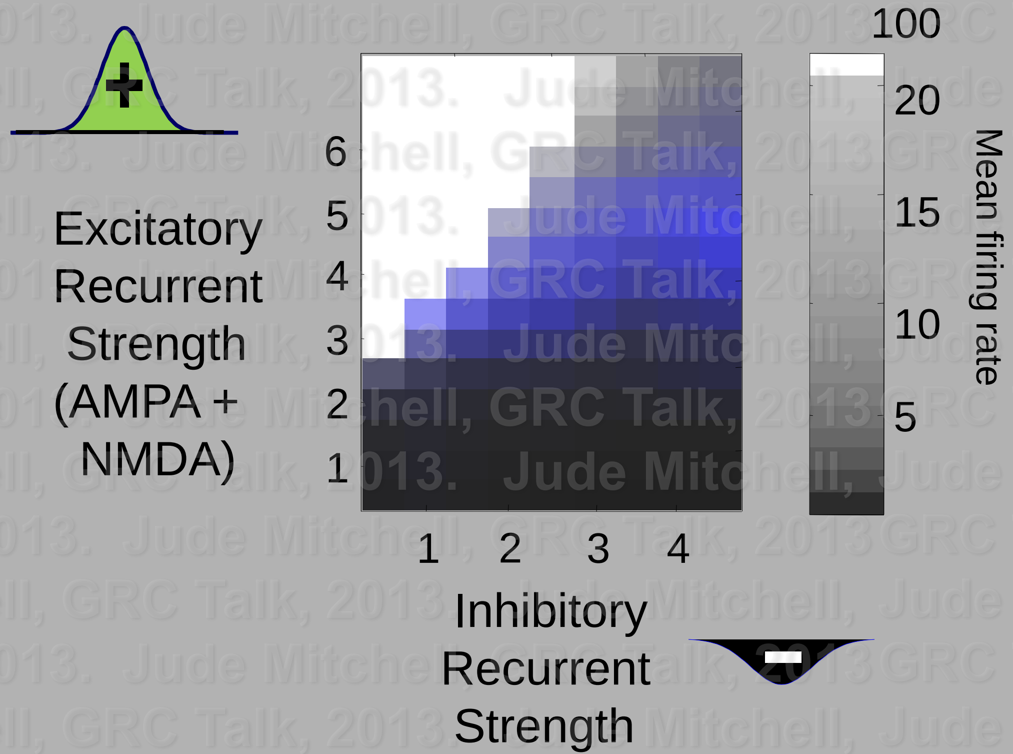



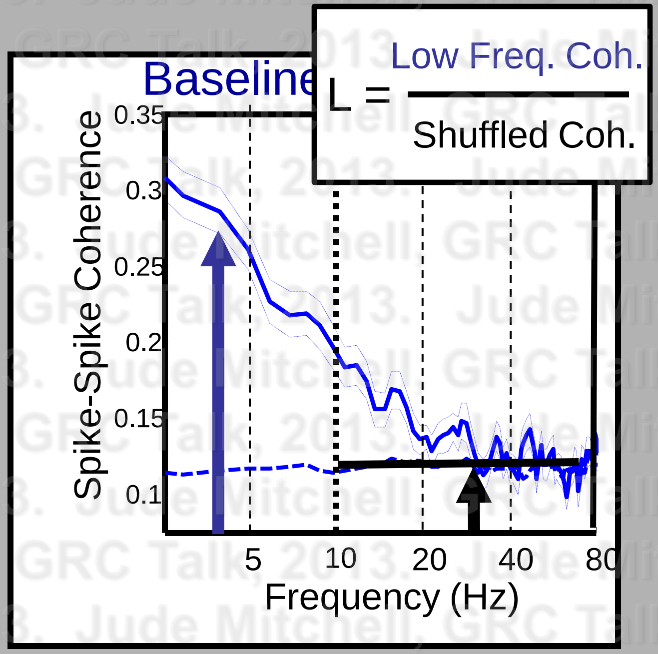
# What model parameters are essential to the shared fluctuations?



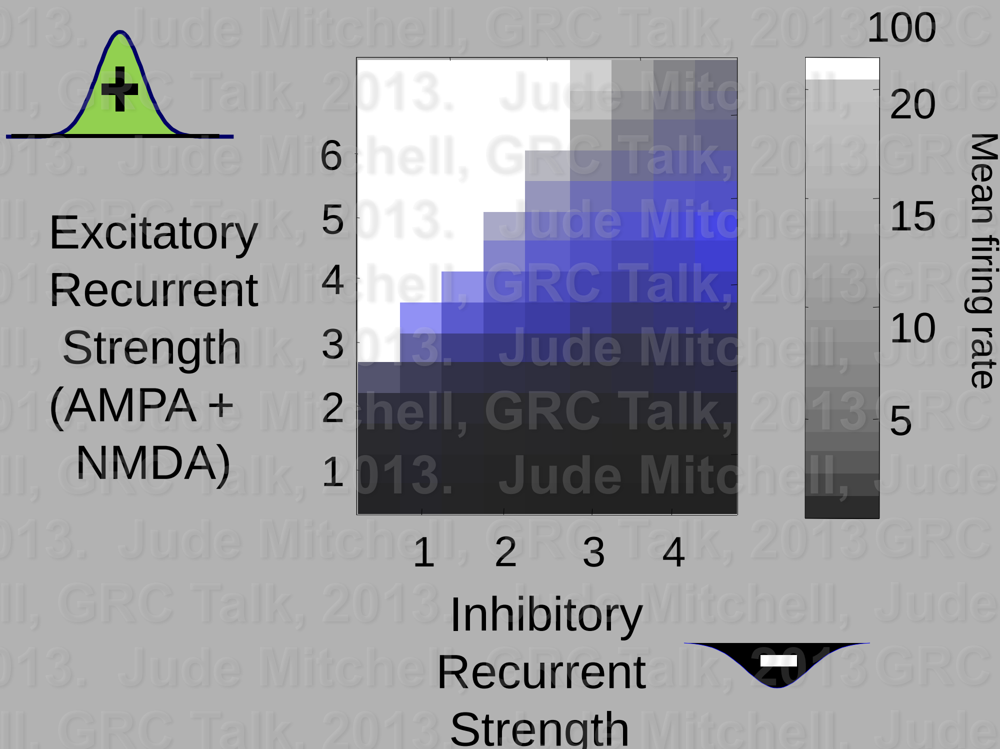



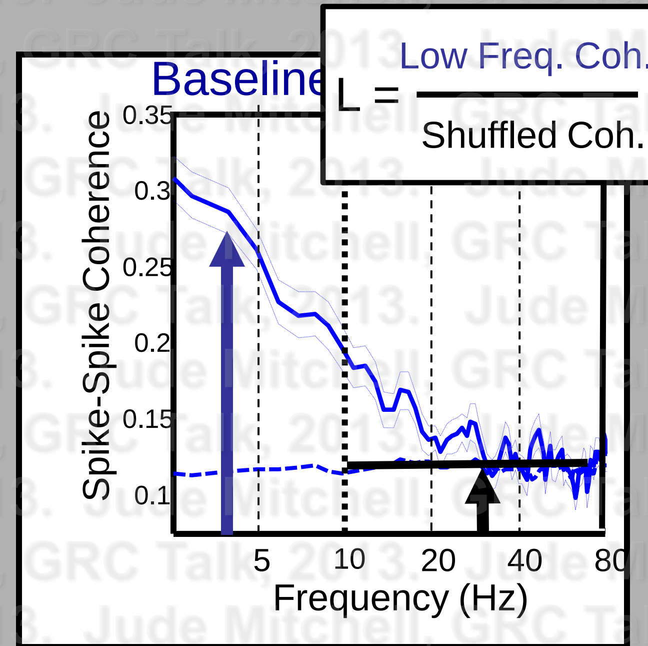
# What model parameters are essential to the shared fluctuations?



# What model parameters are essential to the shared fluctuations?




- strong recurrent connections
- balanced excitation/inhibition
- slower NMDA currents

# Why Does Visual Input Reduce Intrinsic Activity Fluctuations?

$$\tau \; dV/dt \;=\; g_{FF}\,(E_{FF} - V) + g_{REC}\,(E_{REC} - V)$$

$$V_{\infty} \;\cong\; \frac{g_{FF}\,E_{FF} + g_{REC}\,E_{REC}}{g_{FF} + g_{REC}}$$

Normalization = Weighted Averaging
Feed-forward vs Recurrent Terms